Seed dispersal mutualisms and plant regeneration in New Zealand alpine ecosystems

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ABSTRACT

The New Zealand alpine zone has many fleshy-fruited plant species, but now has a relatively depauperate animal fauna. The key question is, therefore, are native alpine plants still being dispersed, if so where to and by what? I first measured fruit removal rates among nine common species using animal-exclusion cages to compare natural fruit removal by all animals, and by lizards only. Over two years, mean percent of fruit removed by early winter ranged from 25–60% among species. Speed of fruit removal also varied depending on species. Secondly, I quantified which animals disperse (or predate) seeds of those fruits, into which habitats they deposit the seeds, and the relative importance of each animal species for dispersal, in two ways. A 2-year study using fixed-area transects to monitor faecal deposition showed that introduced mammals (especially possums, rabbits, hares, sheep, pigs and hedgehogs) were abundant and widespread through alpine habitat. Of the 25,537 faeces collected, a sub-sample of 2,338 was dissected. Most mammals dispersed most (> 90%) seeds intact. However, possums (numerically the important disperser) moved most seeds into mountain beech (*Nothofagus solandri)* forest, while rabbits, hares, and sheep dispersed seeds mainly into open grassland dominated by thick swards of exotic grasses (e.g. *Agrostis capillaris* and *Anthoxanthum odoratum*); all are less suitable microsites. Kea (*Nestor notabilis*), the largest and most mobile of only three remaining native alpine bird species, are potentially useful as a long-distance seed disperser, even though parrots are typically seed predators. I found that kea are numerically more important than all other birds combined, damage very few seeds, and are probably responsible for most dispersal of seeds between mountain ranges. Finally, I investigated the effects of seed deposition microsite (shady/high-light), pulp-removal (whole/cleaned), competition (soil dug/not-dug) and predation (caged/ not) on germination, growth and survival of eight subalpine plant species. There were strong positive effects of shady microsites for seed germination and seedling survival to 3.5 years for six of the eight species. Effects of other treatments were less important and varied among species and stages. Hence, both native birds and introduced mammals are dispersing alpine seeds, but the mammals often deposit seeds in habitats unsuitable for establishment. Any evaluation of the dispersal effectiveness of frugivores must consider their contribution towards the long-term success for plant recruitment through dispersal quantity and quality.

PREFACE

The overall objective of this thesis is to investigate whether seed dispersal mutualisms are functioning in the New Zealand alpine flora. I attempt to answer this broad question in four main data chapters. These chapters (Chapters 2-5) have been written as stand-alone scientific papers and are very closely interrelated. Each paper has been written so that it can be read independently. As a consequence, in order to provide the relevant background within each chapter, there is inevitably a small amount of repetition between them. The introductory chapter (Chapter 1) gives a broad overview of the background to seed dispersal, the New Zealand situation, the rationale behind this research and finally an introduction to the general topics covered in this thesis. Chapter 4 has been published in the journal *Biological Conservation*, but is formatted and presented as for the rest of the thesis for consistency (the published version is also provided in the final Appendix A1). Chapter 4 (referred to as Young et al., 2012) was published in collaboration with both of my supervisors, but the field work, analysis and writing presented in it were predominantly my own. DK and XJN assisted with revising drafts of the manuscript to prepare it for publication. A 'Short Note' article has also been published in *Notornis* (Young and Bell, 2010 - attached in the final Appendix A2), but is not presented as a main chapter in this thesis. All other data chapters are in preparation for submission to journals. Figures and tables are numbered from the beginning within each chapter, while all references are provided at the end of the thesis to avoid repetition. Most of the data chapters have appendices because I intend to include these as supplementary material when I submit the manuscripts for publication.

This research was carried out with a Low Impact Research and Collection Permit from the New Zealand Department of Conservation (National Permit Number: CA-24981-FLO).

"… no one not in the secret could guess that on the high mountains there existed a floral world very different from that of everyday New Zealand, or, indeed, from that of any other land."

Leonard Cockayne, 1910

CHAPTER ONE

Introduction

Kea - mountain parrot with Aoraki Mt Cook in the background (Photo: L.M. Young).

Introduction to seed dispersal

Dispersal of offspring away from the natal site is one way genes move through a population or into new populations (Willson and Traveset, 2000) influencing demography (Harper, 1977), genetic structure, and spatial distribution of future generations (Jordano and Godoy, 2002). For sessile organisms like plants, seeds are dispersed by a variety of mechanisms, both abiotic (e.g. wind, water and gravity) and biotic (via animals). Seed dispersal by animals is achieved either internally through ingestion of fruits and subsequent excretion of seeds (endozoochory) or externally through the attachment of seeds to an animal's coat (epizoochory) (van der Pijl, 1982). The propagules of endozoochorous plant species have a fleshy fruit or similar fleshy component formed from various parts of the floral structure that acts as a reward to frugivorous animals (Ridley, 1930; van der Pijl, 1982, Webb and Simpson, 2001). Because plants benefit by having their seeds moved and animals gain a food reward, endozoochorus seed dispersal by frugivorous animals is a mutualistic interaction (Ridley, 1930; Herrera, 2002). Throughout this thesis, I use the term "seed" in a functional sense to refer to the diaspore (seed plus any invested structures).

Vertebrate animals are important seed dispersal agents for plants (Herrera and Jordano, 1981) with birds most commonly being associated with seed dispersal (van der Pijl, 1982). Many types of mammals are also known to be important seed dispersers. These include primates (Valenta and Fedigan, 2009), elephants (Dudley, 2000), bats (Ingle, 2003), ungulates (Ramos et al., 2006) and even carnivores (López-Bao and González-Varo, 2011; Jordano et al., 2007). Increasingly, other animals such as tortoises (Jerozolimski et al., 2009), fishes (Galetti et al., 2008), and lizards (Wotton, 2002; Traveset and Riera, 2005) are being recognized as important and legitimate seed dispersers. Among invertebrates, crabs (Staddon et al., 2010), ants (especially subfamilies of the Formicidae) (O'Dowd and Hay, 1980), orthopterans (Duthie et al., 2006) and earthworms (Willems and Huijsmans, 1994) are also known seed dispersers.

Why is endozoochorus seed dispersal important?

Through the heterogeneous distribution of seed by frugivores, dispersal can influence patterns of plant survival and establishment (Godinez-Alvarez et al., 2002), community composition (Levin et al., 2003) and genetic structure (Jordano and Godoy, 2002), and can ultimately determine the spatial structure of plant populations (Nathan and Muller-Landau, 2000). There is no universally accepted definition of endozoochorus seed dispersal, but in a

recent review on the effectiveness of seed dispersal, Schupp et al. (2010) define it as the horizontal movement of a seed by an animal from the place it was encountered. Seed dispersal needs to be effective, that is, seeds are not only dispersed, but dispersal results in successful establishment of new individuals (Janzen, 1970; Schupp et al., 2010). Therefore, seed dispersal is a complex, multi-stage process and its overall success is dependent on traits of the dispersal agent (Jordano et al., 2007), plant traits and a variety of other ecological variables, such as microsite and dispersal distance.

Frugivores can differ in seed dispersal effectiveness and contribute to dispersal and long-term plant fitness in myriad ways (Jordano et al., 2007; Lomascolo and Schaefer, 2010). The seed dispersal effectiveness framework (SDE) (Schupp, 1993; Schupp et al., 2010) structures our current thinking about what the process of seed dispersal contributes to the successful recruitment of plants. I use this framework throughout this thesis. Briefly, seed dispersal effectiveness includes both quantitative and qualitative aspects (Schupp, 1993). Quantitative seed dispersal considers numbers of fruits consumed and seeds dispersed, while qualitative seed dispersal incorporates where and how far seeds are dispersed, effects of gut passage and other disperser traits. Spatial patterns of seed deposition can vary with disperser type, behaviour, foraging and movement patterns in space and time, as well as the dynamics of digestive processes, such as gut retention time and seed treatment (Calviño-Cancela, 2002; Jordano et al., 2007).

Seed dispersal in New Zealand

The New Zealand indigenous seed plant flora contains 105 families, 360 genera and around 2000 species (Wilton and Breitwieser, 2000; Gordon, 2012). Of these, an estimated 250-330 plant species in 85 genera and 50 families possess fleshy fruits (Lee et al., 1991; Thorsen et al., 2009), suggesting they are adapted for seed dispersal by frugivores. Fleshy-fruited species are therefore a conspicuous part of the New Zealand flora, but not unusually more common compared with other temperate floras as a whole. For example, compared with New Zealand podocarp (28%) and *Nothofagus* (27%) forests, fleshy-fruitedness in North American coniferous forests (32%) and broadleaf forest (35%), Australian forests and dry woodlands (17-21%) is lower, while mainland temperate forests of Chile and Argentina (ca. 42%) are higher than in New Zealand (Lord, 1999). However, New Zealand does have an unusually high percentage of fleshy-fruited species in alpine communities (12%) (Lord, 1999) and in the woody flora (Burrows, 1992; Lord et al., 2002; Kelly et al,. 2010). Because of geographic isolation, the New Zealand flora has, until recently, had an unusual frugivore

assemblage with almost no mammalian influence (Lord et al., 2002). Instead, it co-evolved in the presence of a largely avian fauna (Holdaway, 1989, Lee et al., 2010), with possible influence by bats, lizards (Whittaker, 1987; Wotton, 2002; Lord and Marshall, 2001) and weta (large flightless Orthopterans) (Burns, 2006; Duthie et al., 2006). The smaller size of the New Zealand frugivore assemblage compared with Australian and South American counterparts has apparently influenced the evolution of fruit size and shape (smaller and less round) in congeneric species of colonizing taxa, sometimes within a relatively short evolutionary timeframe (Lord, 2004). With respect to the New Zealand flora as a whole, Lord et al. (2002) classify frugivores into three guilds differing in size and ability to access fruits; (1) flightless birds – many large, most extinct, (2) volant birds, both extinct and extant species, and (3) lizards.

Since the relatively recent arrival (ca. 1280 AD) of humans in New Zealand (Wilmshurst et al., 2008), nearly half the avifauna and a significant proportion of the herpetofauna (lizards) have become extinct (Tennyson, 2010), while many extant species have become uncommon or range-restricted (Clout and Hay, 1989). Plant-frugivore relationships are therefore likely to have undergone major changes (Holdaway, 1989; Lee et al., 1991; Thorsen et al., 2009). Other key changes have potentially come about since the introduction of mammalian and avian herbivores into New Zealand, mostly throughout the past few centuries (Kelly et al., 2010). It is difficult to quantify some of these changes, e.g., the flow-on effects of faunal extinctions on seed dispersal, plant distribution and community structure. Consequently, little work has been done on this. For instance, how do we know whether the loss of a frugivorous bird species has led to the reduction in abundance or local extinction of a particular plant species due to the termination of a specialised mutualism? In turn, what effects would this have had on wider community structure and ecosystem function? There is considerable scope in New Zealand to study the potential impacts caused by the loss of indigenous fauna and the replacement by exotic birds and mammals on ecosystem processes such as seed dispersal, particularly in mountain ecosystems where very little is known.

Fleshy-fruited flora and fauna in New Zealand's montane, subalpine and alpine zone

".. There is compensation for the lack of flower colour [of the New Zealand mountian flora] to be seen in the fleshy fruits produced by several mountain genera…"

(Mark and Adams, 1973)

The alpine zone has been generally defined as that which is located between the climatic treeline and the permanent (summer) snowline, below the nival zone (Wardle, 1964; Mark and Adams, 1995: Mark et al., 2000). Fleshy-fruitedness is present in an unusually high proportion of the total alpine flora compared to other temperate alpine plant communities (Lord, 1999). Why are there so many alpine and sub-alpine plants with fleshy fruits yet an apparent lack of dispersal agents? This question provides the major rationale behind this thesis, which is to determine whether these plants are successful in terms of dispersal, germination and establishment with today's depauperate resident alpine fauna.

Many native flightless birds have become extinct in recent history (ca. 700 years ago), both in the forest and above the bushline, and it is likely some of them were important for seed dispersal (Lee et al., 1991). For example, hundreds of intact seeds of 20 fleshy-fruited shrubs (including subalpine *Corokia* and *Coprosma* spp.) have been found in moa gizzards from deposits in North Canterbury (Burrows 1981), and seeds of numerous prostrate and shrubby species have also been extracted from coprolites of six moa species from the Dart Valley (Wood et al., 2008) and other areas (Lee et al., 2010). It seems that most native extinct bird species incorporated at least some fruit and/or seeds in their diet (for an excellent summary of extinct and extant New Zealand avifauna and their broad diet categories see Lee et al. (2010)). However, it is not known which of these extinct birds resided above treeline and consequently, their contribution towards seed dispersal of the subalpine and alpine flora. The kakapo (*Strigops habroptilus*) – a large, flightless parrot – is now extinct on the mainland of New Zealand. Kakapo were once common in the subalpine zone and coprolite evidence shows that they consumed and dispersed some seeds intact (Horrocks et al., 2008). To understand the co-evolutionary relationships between the alpine fleshy-fruited flora and extinct avifauna would be of pivotal importance in order to determine the effects of their loss on plant populations. However, this would require a separate and in-depth study. Here I focus on the extant fauna, including introduced species, and their role in seed dispersal of the subalpine flora.

There remain only three native bird species that principally inhabit the alpine zone in New Zealand; the kea or mountain parrot (*Nestor notabilis*), rock wren (*Xenicus gilviventrus*) and pipit (*Anthus novaeseelandiae*), but almost nothing is known about their seed dispersal effectiveness and whether they are in fact important consumers and seed dispersers of alpine fleshy-fruited plants (but see Clarke, 1970). Numbers of parrots such as kea and sometimes kaka (*Nestor meridionalis*) inhabiting or visiting the alpine vegetation have declined since

human arrival (Elliott and Kemp, 2004). Kea and rock wrens are nationally vulnerable (IUCN, 2011) and populations of both species have been drastically reduced or lost altogether in some areas (Michelsen-Heath and Gaze, 2007; Kea Conservation Trust, pers. comm). Other native birds are known to sometimes visit the alpine areas e.g., bellbird (*Anthornis melanura*), silvereye (*Zosterops lateralis*), tomtit (*Petroica macrocephala*) (Kelly et al., unpubl. data), black-backed gulls (*Larus dominicanus*), and a range of introduced birds including Canada geese (*Branta canadensis*), chukor (*Alectoris chukar*) and magpie (*Gymnorhina tibicen*). Introduced mammals, such as the Australian brushtail possum (*Trichosurus vulpecula*), pigs (*Sus scrofa)*, red deer (*Cervus elaphus*), chamois (*Rupicapra rupicapra*) and Himalayan tahr (*Hemitragus jemlahicus*) also visit or inhabit the alpine zone. Although very little is known about the roles of introduced mammals in seed dispersal of most native flora (Kelly et al., 2010, but see Williams et al., 2000; Dungan et al., 2002), any of the above animals could also ingest seeds of alpine plants contributing either to seed dispersal, seed predation or both.

New Zealand's extant frugivorous birds are generally considered to be generalists (Lord, 2004). While we cannot determine whether any specialised mutualisms have been lost in this system as a consequence of species extinctions, we can try to answer questions relating to present-day animal-plant mutualisms, such as: what is the current suite of frugivorous animals for a given range of fleshy-fruited plant species (including the relative contribution made by both native and introduced animals); how effective are they as seed dispersers or seed predators; and how important are they for dispersal, germination success and growth of the plants?

Thesis outline

The overall objective of this thesis is to understand whether dispersal mutualisms are functioning effectively in the New Zealand montane, subalpine and alpine fleshy-fruited flora under the current novel frugivore assemblage. I attempt to address this broad question to cover the whole spectrum of phases involved in the seed dispersal process (Figure 1.1). Throughout this thesis I operate under the original and revised versions of the seed dispersal effectiveness framework (Schupp 1993; Schupp et al., 2010), focusing on quantitative and qualitative components of dispersal. Throughout this thesis, I use "fruits" in a functional sense rather than a botanical sense, to denote the dispersal unit, i.e. packages made up of seeds plus accessory tissues used as food by animal dispersers, irrespective of their botanical origin (as per Herrera, 1992).

In Chapter 2 I begin with the most basic question from the plant perspective, by asking whether current levels of fruit removal are adequate for alpine fleshy-fruited flora. I quantify fruit removal rates across the entire fruiting duration, from fruit production through until the last ripe fruits remain on parent plants. Over two fruiting seasons I compare levels and speed of fruit removal by different disperser guilds – lizards versus other larger dispersal agents – relative to fruit removal rates under the most extreme scenario: one without dispersers. If frugivore numbers are adequate, we should expect overall levels of fruit removal to be high in open-access plants (i.e. low numbers of ripe and overripe fruit on branches) compared with plants covered by animal-exlcusion cages where we would expect high numbers of ripe and overripe fruits to accumulate over time and eventually fall off below the parent plant.

The remainder of this thesis explores varying aspects of dispersal quality for plant fitness and attempts to incorporate most phases of the seed dispersal process. In Chapter 3, I conduct a community-level investigation into the relative effectiveness of all potential dispersers, focusing on the contribution of introduced mammals in particular, since they are now widespread and abundant in New Zealand's mountains. Very little is known about the role of the majority of exotic mammalian species for seed dispersal in any New Zealand ecosystem and very few studies have utilized a long-term, community-level approach to investigate the relative importance of each disperser for each plant species in a given community. I analyse thousands of faecal deposits collected from fixed-area transects over two fruiting seasons to determine which plant species are being dispersed by each animal, the proportions of seeds dispersed intact versus in fragments, and where faeces are deposited in the landscape by each disperser.

I then investigate the importance of native and exotic birds for seed dispersal and consider the implications of their relative rarity on seed dispersal for the native alpine flora (Chapter 4). There are very few apparent native bird dispersers and resident alpine bird species. The kea is the most widespread and mobile of the handful of alpine resident bird species, although their numbers are declining. Kea have been widely assumed to be a seed predator rather then a legitimate disperser, although this has rarely been tested. I test to what extent kea ingest and defaecate intact seeds from various plant species and their relative importance for seed dispersal in the alpine zone.

In Chapter 5 I consider the importance of dispersal and its inherent qualities for successful germination, survival and establishment of plants using a full factorial field

experiment. I assess which qualities of dispersal are important for each stage of recruitment. I attempt to determine how dispersal failure, seedling herbivory and microsite act alone or synergistically to influence recruitment at each phase. This work is of particular importance in relation to the potential differential contributions by native compared with exotic frugivores in terms of where they deposit seeds. Finally, in Chapter 6 I sythesise the findings from each chapter and assess whether seed dispersal mutualisms are working effectively in New Zealand alpine ecosystems.

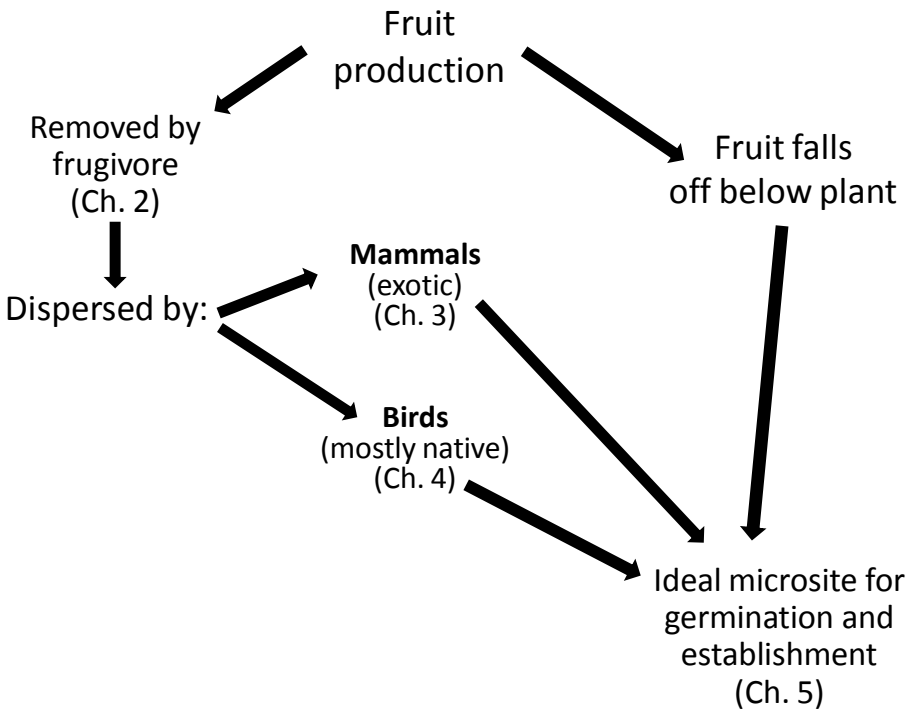
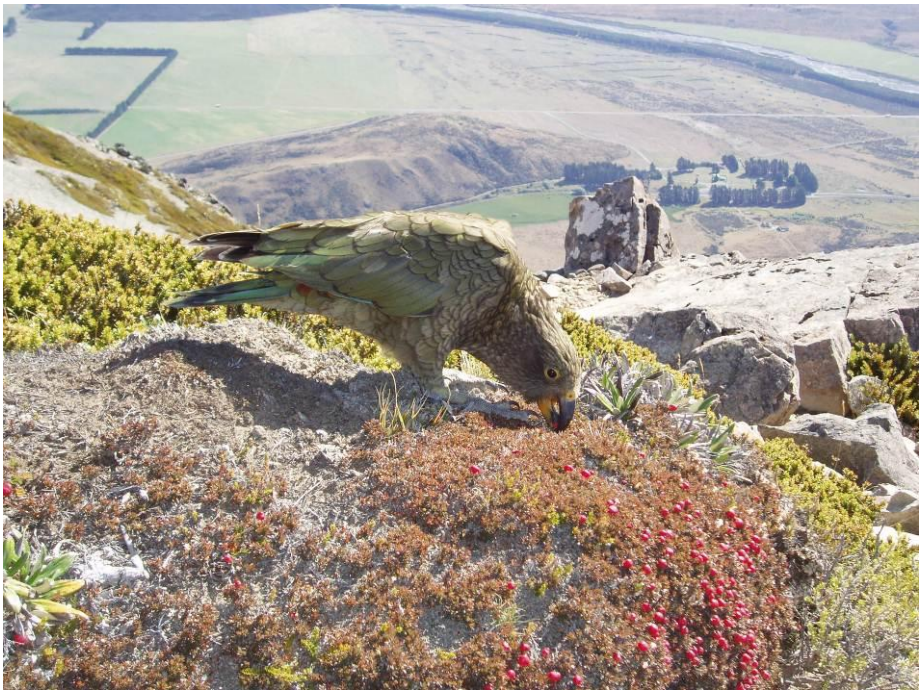


Figure 1.1 Outline of thesis chapters in relation to stages of the dispersal process.

CHAPTER TWO

The current effectiveness of fruit removal and seed dispersal in New Zealand montane and alpine fleshy-fruited plants



Juvenile kea feeding on berries of *Pentachondra pumila* on top of Sugarloaf (1359 m), Cass.

(Photo: L.M. Young)

Abstract

The New Zealand mountain flora is rich in fleshy-fruited species but many terrestrial frugivorous birds are extinct or declining, putting seed dispersal mutualisms at risk. To determine whether fruits are currently being removed by animals, I measured fruit removal rates in nine species of fleshy-fruited alpine plants from a range of families using cages (no animal access to fruit) and control (unmanipulated – open-access to fruit by all animals) plants. In 2008 I used two elevations at Cass, inland Canterbury. For the 2009 fruiting season, seven species were monitored again, but a second site (Temple Basin, Arthurs Pass) and a lizard-only cage access treatment were added. Fruit removal under the current suite of available native and exotic frugivores varied depending on species. Overall mean percent fruit removal ranged from 25-60% in open-access treatments, 21-33% in lizard-only treatments and 2-22% in animal-exclusion cage treatments. The largest difference in mean final percent fruit removal between open-access and cage treatments was for the montane shrub *Aristotelia fruticosa* (60.3% vs 2.6% respectively). The lowest levels of fruit removal were around 25% for the montane shrub *Corokia cotoneaster* and alpine shrubby conifer *Podocarpus nivalis*. There was little difference in final percent fruit removal between lizard-access cages and all-animal exclusion cages at Temple Basin, suggesting that fruit removal by lizards was not important at that site. Some evidence for lizard frugivory occurred at Cass with fruit removal levels intermediate between open and cage treatments. It has been suggested in previous literature, that delays in fruit removal may have no fitness consequences, as long as fruits are being removed at some point before they rot and fall below the parent plant. In this respect, mean overall percent fruit removal levels seen in this study (25-60%) by available seed dispersers can thus be regarded as adequate.

Introduction

Fleshy-fruited plants rely on animals to eat their fruits and disperse their seeds. Frugivorous animals affect seed dispersal through the number of fruits they remove, and through where and in what condition seeds are dropped (Loiselle and Blake, 1999; Jordano and Schupp, 2000; Wenny, 2000). Without fruit consumption by animals, dispersal and recruitment would be greatly reduced. Although consumption may not always result in effective seed dispersal (Chapman and Chapman, 1995, Cordeiro and Howe, 2001), it is reasonable to assume a general increase in dispersal with increased fruit consumption

(Wenny, 2003). Monitoring fruit removal and removal rates over time is thus an informative measure of seed dispersal from the plant perspective.

In New Zealand, many terrestrial frugivorous bird species are extinct (Holdaway, 1989; Tennyson, 2010) or declining (Hitchmough et al., 2007) possibly putting mutualisms such as seed dispersal at risk (Clout and Hay, 1989; Kelly et al., 2010). The montane, subalpine and alpine flora (hereafter montane and alpine for simplicity) of New Zealand is relatively rich in fleshy-fruited plant species from many different and diverse families (Lord, 1999). Despite the prevalence of fleshy fruit in the subalpine flora, there are few obvious native frugivorous animals to disperse their seeds. Native bird dispersers in the Southern Alps of New Zealand are now probably restricted to a handful of species, including kea (*Nestor notabilis*) and occasionally pipit (*Anthus novaeseelandiae*) (Clarke, 1970; Young et al., 2012), falcon (*Falco novaeseelandiae*) (Young and Bell, 2010, Appendix 2), rock wren (*Xenicus gilviventrus*), and infrequent forest birds. Native lizards (Whittaker, 1987; Lawrence, 1997), and introduced birds (Clarke, 1970) and mammals may also act as dispersal agents for seeds of alpine fruits.

Very little is known about the effectiveness (quantity and quality) of lizards in seed dispersal of most New Zealand flora (but see Wotton, 2002), except that some lizards are known to ingest some fruit and excrete viable seed of several montane grassland species (Whittaker, 1987; Lawrence, 1997). Even less is known about the lizard fauna and ecology of areas such as Arthurs Pass National Park (Lettink pers. comm; Department of Conservation Herpetofauna Database). Two lizard species are recorded in the Cass area to date: the Southern Alps gecko (*Woodworthia* "Southern Alps") and and the common skink (*Oligosoma polychroma*). There has been much speculation about some fruits being lizard-adapted (e.g., *Melicytus alpinus* (Whittaker, 1987; Lawrence, 1997)), although there is currently little evidence supporting this.

This apparent lack of native dispersers thus begs the question of whether alpine fruits are being adequately removed by animals so that seed dispersal mutualisms are still functioning effectively. If frugivore numbers are low, we might see many fruits becoming overripe later in the fruiting season, and falling off directly beneath parent plants. In comparison, with adequate numbers of frugivores present, high fruit-removal rates with low numbers of ripe and overripe fruits should be expected. The proportion of ripe or overripe compared to unripe (green) fruit is an approximate index of dispersal service (Roberston et al., 2008) but overall percent of fruit removed can also be used. Cages of varying mesh size

can be used to exclude animals of varying body size to determine the relative removal rates of different dispersal agents by allowing only species smaller than the mesh size to enter. The natural rates of fruit removal (no cage: open-access to all potential frugivores) can then be measured against the worst case scenario situation (cage that excludes all animals), where no fruit removal would occur, against rates of fruit removal using cages to exclude animals larger than lizards.

In many areas of the Southern Alps, natural treelines have been lowered due to both natural and anthropogenic disturbance such as wind-throw, tree and rock falls, avalanches, grazing and fire over the past 1000 years (Wardle, 1991). Natural treeline elevations range from ca. 1400 m a.s.l. in the northern South Island, down to 900 m a.s.l. in the south. Subalpine grasslands and shrublands have effectively replaced many *Nothofagus* forests in these areas, particularly east of the Main Divide of the Southern Alps. It is thus valuable to look at fruit removal rates at both their natural (high elevation) sites and lower elevation sites as perhaps potential disperser fauna change along an altitudinal gradient.

A large variety of fruit colours is represented, including white (or transparent), red, pink, orange, yellow, blue, purple, black and flecked (see Table A1 in Young et al., 2012 (Chapter 4) for a detailed summary of alpine plant fruit traits at the sites). Fruit colour polymorphisms between individual plants within a species are also a prominent feature of the mountain flora, particularly for species within the family Ericaceae. In fact, for some species, fruit can appear in a wide range of colours rather than just two (which is more common).

Figure 2.1 Fruit colour polymorphisms in the divaricate shrub *Coprosma propinqua*, all growing within 100 m of each other at Cass.

Two striking examples include the montane divaricate shrub *Coprosma propinqua* (Rubiaceae), and the dwarf heath *Leucopogon colensoi* (Ericaceae). In *C. propinqua*, fruit

colours span the spectrum from white, blue, purple, black and flecked, through to yellow (Figure 2.1). In *L. colensoi*, fruit colours range from (most commonly) red to (least commonly) white and all shades of pink and crimson in between (Figure 2.2). There is little known about the ecological and evolutionary significance of fruit colour polymorphisms and their maintenance, both in the New Zealand mountain flora and in general. Willson and Whelan (1990) review various non-exclusive hypotheses relating to the evolution and maintenance of fruit colour. These include that: birds select red and black fruits over orange and yellow or lighter coloured fruits, and select certain colours because of their long-distance conspicuousness to frugivores (Willson and Whelan, 1990) or conspicuousness against their natural background (Lee et al., 1988). Other authors have tested hypotheses ranging from fruit traits responding to selective pressures exerted by various frugivores (Willson and Whelan, 1990), genotypic or pleiotropic effects of fruit colour alleles (Whitney and Stanton, 2004), and habitat heterogeneities (Bach and Kelly, 2007). One key assumption of many of these hypotheses is that different fruit colours might be removed at different rates. This has not been quantified, particularly in the New Zealand montane and alpine zone.

Figure 2.2 Fruit colour polymorphs for *Leucopogon colensoi* with red and whitish fruits and multiple coloured fruits of two different plants growing interspersed with each other at Cass.

The main objective of this study is to determine the effectiveness of current seed dispersal by investigating fruit removal for nine species of fleshy-fruited subalpine plant species, including one with polymorphic fruit colour. Specific questions I will attempt to answer include: (a) Are seeds from montane to alpine plants being eaten and removed by animals? (b) How does fruit removal differ between caged and uncaged treatments (i.e. open-access to all dispersers versus lizard-access only, versus no disperser access)? (c) How does fruit removal vary with species, site, elevation and year? (d) What is the fate of fruit over time and what are the relative proportions of fruit that are removed versus become overripe

and subsequently, undispersed? (e) Are there differences in fruit removal rates between red and white coloured fruit in *L. colensoi*?

Methods

Study sites, vegetation and potential dispersers

Field work was conducted at two sites – Cass (43° 2' S, 171 ° 47' E), 5 km east of the Arthurs Pass National Park eastern boundary, and Temple Basin (42° 54' S, 171° 34' E), within Arthurs Pass National Park, both in the Canterbury region, South Island, New Zealand. Both sites are characterised by areas of open high-country grassland, mixed scrub/shrub, herbaceous and mat plants interspersed with scree and rock, incorporating similar habitat at lower (montane) altitudes as low as 650 m a.s.l with a lowered treeline and small remnant forest patches due to burning. Cass is considerably drier than Temple Basin with a mean annual rainfall of around 1300 mm while Temple Basin which is right on the Main Divide of the Southern Alps has 5000 mm. The vegetation at Cass is characterised by open grassland dominated by native fescue tussock (*Festuca novae-zealandieae*) and exotic grasses (*Agrostis capillaris* and *Anthoxanthum odoratum*), interspersed with mixed low-growing, dry-fruited shrubs including manuka (*Leptospermum scoparium*: Myrtaceae), matagouri (*Discaria toumatou*: Rhamnaceae), tawini (*Ozothamnus leptophylla*: Asteraceae); hebe (*Hebe brachysiphon*: Scrophulariaceae), and fleshy-fruited shrubs such as *Coprosma propinqua*, *C. intertexta* and *C. dumosa* (Rubiaeceae), *Melicytus alpinus* (Violaceae), and snow totara (*Podocarpus nivalis*: Podocarpaceae). Many other low-growing, prostrate or sprawling mat plants are also present, many with fleshy fruits. At Temple Basin, vegetation at lower elevations is dominated by shrubby taxa such as *Dracophyllum*, *Hebe*, and *Coprosma* species among low-growing podocarps such as *P. nivalis*, pygmy pine (*Lepidothamnus laxifolius*), and bog pine (*Halocarpus* spp.) with mountain toatoa (*Phyllocladus alpinus*: Phyllocladaceae). Little is known about the lizard fauna the sites, particularly Temple Basin. For other potential bird and mammal dispersers present at the sites, see Chapters 3 and 4.

Study plants

At least 50 native fleshy-fruited plant species within 24 genera and 14 families occurred at the sites. All fruits contained small seeds 0.4 to 6.0 mm length within small fruits up to 12 mm (see Appendix 1 in Young et al., 2012, Chapter 4). Nine species were selected for this study, representing a range of plant families, fruit colours, shapes and sizes.

Fruit removal rates and treatments

For species with a wide altitudinal range, replicates were set up at both high and low altitude sites in order to make comparisons between fruit removal at varying elevations. All fruit removal experiments were performed at only Cass in 2008. Another site (Temple Basin) was introduced in 2009 to compare fruit ripening and removal with those at Cass. The sites differ in vegetation, conservation status, altitude, history and rainfall (see Burrows, 1977 and Chapter 3 for more detail). See Table 2.1 for outline of species, sites, years, treatments and other detail of fruit fate study included in this chapter.

Table 2.1 Species, fruit colour, sites and treatments used in fruit removal experiments over two fruiting seasons.

Species	Family	Fruit colour used	2008 [a]	2009 [a]
Corokia cotoneaster	Argophyllaceae	Red/Orange	Cass L,H	-
Aristotelia fruticosa	Elaeocarpaceae	Pink/Red	Cass L	-
Pentachondra pumila	Ericaceae	Red	Cass H†	Cass H; Temple L,H†
Gaultheria depressa	Ericaceae	White	Cass L,H	Cass L,H; Temple L,H
Leucopogon colensoi	Ericaceae	Red	Cass L,H	Cass L,H
Leucopogon colensoi	Ericaceae	White	Cass L,H	Cass L,H
Podocarpus nivalis	Podocarpaceae	Red	Cass L*,H	Cass L,H; Temple L,H
Muehlenbeckia axillaris	Polygonaceae	White	Cass L	-
Coprosma propinqua	Rubiaceae	Blue	Cass L,H	Cass L,H
Coprosma petriei	Rubiaceae	Pale blue	Cass L	Cass L

Footnotes: [a] Treatments in 2008 = cage and open; in 2009 = cage, open and lizard cage. Replicates = 5 per species/season/altitude (except † = 4 and * = 6). L = low, H = High altitude sites. A dash means not studied in that season.

During the start of the fruiting season (usually ca. January), branches or parts of plants with more than 50 fruits were tagged. (Most had more than 200 fruits to ensure large enough numbers would account for any losses occurring during counting when fruits were sometimes accidently knocked off). Fruit fates were followed over time throughout the fruiting season (between 4-6 months) to determine the fate of fruits under situations of zero frugivore activity vs. normal frugivore activity. The numbers of unripe, ripe, overripe, dead or aborted and fallen fruits were counted approximately every four weeks in both treatments and removal rates were calculated.

Unripe fruits for all species were green, hard and smaller than mature fruit. I defined fruit as being ripe (available to be eaten) when the colour had largely changed from green to its mature colour (species-dependent), and the fruit pulp had softened and become sweeter (to the human taste). Overripe fruits became less fleshy and developed wrinkles, and were

generally considered to be less attractive for frugivore selection. The fraction of fruits going from unripe to overripe during the 4-6 months in the absence of dispersal or predation could be determined from the monthly counts. Fruits in the "gone from the plant" category were kept separate from fruits which had fallen off either into mesh bags (on bagged treatment branches) or fallen to the ground - where fruit pulp had shrivelled away leaving only seeds remaining exposed, (usually on top of the foliage for mat-forming species such as *C. petriei*). Because fruits in the "fallen" category were very hard to account for, mostly due to the difficulties in accurately counting fallen fruits beneath or within foliage, results in this category are likely to be majorly underestimated. Consequently, the calculations for "total percent of fruit removed" are likely to be overestimated in the cage treatments (which should be zero). If frugivore visitation was adequate, we would expect lower numbers of ripe and overripe fruits on open-access treatments compared with high numbers of ripe, overripe and accumulated fallen fruits for plants in caged treatments.

Two of the fruiting species used in this study posed complications for the analysis. *Pentachondra pumila* and *M. axillaris* appeared to flower continuously until late in summer/early autumn, suggesting that unripe fruits would continue to appear throughout summer and autumn if pollination and fruit set were successful. This made fruit ripening and fruit removal measurements very difficult, particularly for *M. axillaris*; hence this species was only used in the 2008 season. For *P. pumila*, flower numbers were easier to count and monitor. Therefore, I counted flowers and fruits over time for *P. pumila* and used this species in 2008 and 2009.

2008 fruiting season

Branches were assigned to one of two treatments – caged to exclude all frugivores (cage) and open-access to any frugivore (control). For shrubby species, tagged branches for the two treatments were usually located within an individual plant, but for prostrate plants, treatments were placed on different plants within five metres of each other. Cages for prostrate plants (mesh size 4 mm) or muslin bags for shrubs (mesh size 1 mm) were applied to branches after flowering, or at the 'green fruit' stage, (between December and February depending on species and altitude). For some species, there were already low levels of ripening fruits by the time the experimental setup was complete.

2009 fruiting season

In 2009, the same experiments were performed but an extra treatment was added to test whether lizards were removing fruit and how this compared with fruit removal rates in cage and open-access treatments. Cages with 2.5 cm mesh size, large enough to allow lizard access while excluding all other animals, were added to branches or sections of mat plants in the same fashion as the previously described.

Statistical Analysis

Generalized linear models (GLMs) were used to test for differences in fruit removal rates between levels of animal exclusion treatments, sites, years and altitudes across the fruiting period using plants as replicates. The response variable used in analyses for each species was the final proportion of fruit removed at the last count in the fruiting season (usually May or June, but for high altitude treatments at Temple Basin, the last count was in April just before heavy snowfalls). The response variable was binomial (final proportion of fruit removed out of the maximum number of fruit present at the start of the study). *A priori* tests showed data were overdispersed therefore a quasibinomial error term was specified.

Results

Overall fruit removal

The animal-exclusion cage treatment strongly reduced fruit removal for all species except *P. nivalis*, *C. petriei* and *M. axillaris* (Table 2.2 and 2.3). For these three species, levels of fruit removal were not significantly higher in open-access treatments relative to cage treatments, suggesting either fruit removal levels truly were low under natural conditions, or that there were some difficulties in monitoring fallen fruits inside the cage treatment, (thereby suggesting that fruits were removed when they actually weren't). For species where fruit removal was significantly higher under natural conditions than cage treatments, *A. fruticosa* showed the largest difference between treatments, with mean fruit removal in open-access treatments 58 percentage points higher than cage treatments. Open-access treatments in *L. colensoi*, *G. depressa* and *P. pumila* all had around 25% higher overall fruit removal than cage-treatments and likewise, just under 20% for *C. cotoneaster* and *C. propinqua*. For all species, mean percent fruit removal in lizard-only treatments fell somewhere in the middle between open-access and cage treatments (Table 2.3).

Table 2.2 Significance, residual d.f. and percent deviance explained by each predictor variable for overall percent fruit removal at the final count of the fruiting season(s). Summary statistics presented for each species were obtained from quasibinomial generalized linear models using Chi-squared tests.

Species	Predictors	df	Deviance	Resid. df	Resid. dev	% dev. expl.	P-value	Signif.
G. depressa	NULL			319	19713			
	year	1	188.6	318	19524	0.96	<0.05	*
	site	1	569.7	317	18954	2.92	<0.001	***
	altitude	1	19.5	316	18935	0.10	0.5	
	treatment	2	1695.4	314	17239	8.95	<0.001	***
P. nivalis	NULL			279	9011.8			
	year	1	207.3	278	8804.5	2.30	<0.05	**
	site	1	560.5	277	8244	6.37	<0.001	***
	altitude	1	12.1	276	8231.9	0.15	0.49	
	treatment	2	131.9	274	8100	1.60	0.07	.
P. pumila	NULL			190	8636.5			
	year	1	127.4	189	8509.1	1.47	0.05	.
	site	1	40.3	188	8468.8	0.47	0.27	
	altitude	1	1.0	187	8467.8	0.01	0.86	
	treatment	2	1423.3	185	7044.5	16.81	0.00	***
C. propinqua	NULL			227	14718			
	year	1	0.2	226	14718	0.00	0.95	
	altitude	1	1.7	225	14716	0.01	0.86	
	treatment	2	1226.8	223	13490	8.34	<0.001	***
C. petriei	NULL			103	6360.6			
	year	1	62.9	102	6297.7	0.99	0.28	
	treatment	2	14.1	100	6283.6	0.22	0.88	
C. cotoneaster	NULL			99	4329.5			
	altitude	1	19.2	98	4310.3	0.44	0.48	
	treatment	1	531.0	97	3779.4	12.32	<0.001	***
A. fruticosa	NULL			39	3127.8			
	treatment	1	1453.4	38	1674.4	46.47	<0.001	***
M. axillaris	NULL			35	3160.9			
	treatment	1	119.9	34	3041.1	3.79	0.19	
L. colensoi	NULL			421	35497			
	year	1	1.4	420	35496	0.00	0.88	
	altitude	1	13.9	419	35482	0.04	0.64	
	treatment	7	5502	412	29980	15.51	<0.001	***

For *G. depressa* there was also a significant effect of site and year on overall rates of fruit removal (Tables 2.2 and 2.3). Mean percent of fruit removed was higher at Cass than Temple Basin and higher in the 2009 fruiting season than in 2008.

For *P. nivalis* it appeared that overall fruit removal rates were low, with no significant difference in mean percent fruit removal between open, cage and lizard-only cage treatments (Table 2.2). This is possibly due to the significant site effect, where levels of fruit removal were not much better in open-access than in cage treatments at Temple Basin. When Cass data were analysed alone for *P. nivalis*, there was significantly higher mean percent fruit removal for open-access compared with cage treatments at that site (Quasi-binomial GLM: $F_{(2,170)} = 3.2$, $p = 0.04$).

There was no significant effect of altitude on fruit removal for any species (Table 2.2 and 2.3). The effects of fruit colour on fruit removal are presented separately (see Fruit colour polymorphism section below).

Table 2.3 Summary table showing species comparisions of significant effects and overall mean percent of fruit removed by the last fruit count in the season(s). Final treatment mean values presented below are taken from all replicates and include all variables regardless of site, year, and altitude. NA signifies that predictor was not used for that particular species. Significant site effects show which site was greater (C = Cass, T = Temple Basin).

	Statistically significant effects				Overall treatment mean % removed (± se)		
Species	Year	Site	Altitude	Treatment	Cage	Lizard	Open
G. depressa	*	*** C>T		***	21.8 ± 2.6	33.1 ± 3.8	45.6 ± 3.6
P. nivalis	**	*** C>T			21.8 ± 2.3	21.2 ± 2.7	24.8 ± 2.6
P. pumila				***	20.4 ± 3.4	30.9 ± 4.4	43.5 ± 4.1
C. propinqua		NA		***	13.8 ± 2.0	23.7 ± 4.3	31.4 ± 3.3
C. petriei	NA	NA			24.6 ± 4.7	23.6 ± 7.2	29.1 ± 5.3
C. cotoneaster		NA		***	8.6 ± 2.2	NA	26.4 ± 4.5
A. fruticosa	NA	NA		***	2.6 ± 0.9	NA	60.3 ± 9.2
M. axillaris	NA	NA			43.7 ± 8.4	NA	55.8 ± 10
L. colensoi		NA		***	16.3 ± 1.7	24.1 ± 2.9	42.6 ± 3.0

Fruit ripening and removal over time

Because information on fruiting phenology such as ripening and speed of removal were not a central focus of this chapter, the results in this section are restricted to only one

species as an example. *Gaultheria depressa* was selected to show rates of fruit ripening and removal over each fruiting season since there were significant differences in final percent fruit removal between sites, years and treatments (Figures 2.3, 2.4, 2.5, Table 2.3). The top two graphs in each set of figures represent the open-access treatment for Cass 2008 (Figure 2.3), Cass 2009 (Figure 2.4) and Temple Basin 2009 (Figure 2.5), and show the highest levels of grey through time (percent of fruit gone). Numbers of overripe fruits were generally lower for cage treatments (purple), with increased numbers of fallen fruits (black), but the numbers of fallen fruits are likely to be underestimated due to difficulties in counting them in cages.

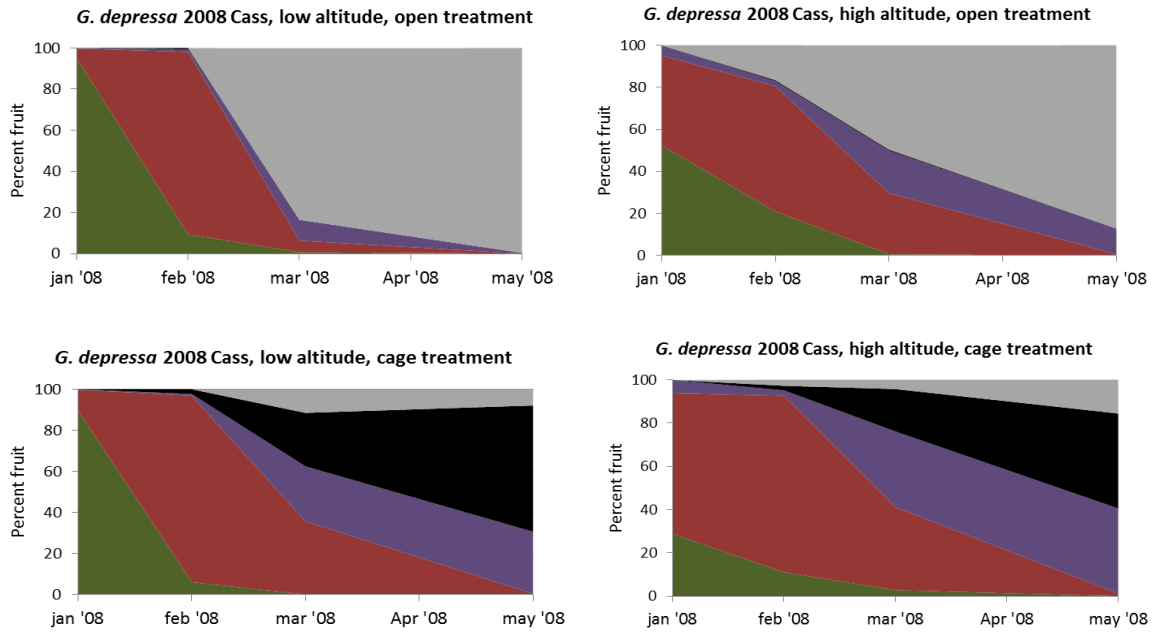


Figure 2.3 Fruit ripening and removal rates over time for *Gaultheria depressa* during the 2008 fruiting season at Cass for low (n=5) and high (n=5) altitude plants under open-access (n=5) and cage (n=5) treatments. Total percentage of fruits in each category: green = unripe, red = ripe, purple = overripe, black = fallen, grey = gone.

All graphs on the left hand side of all figures show low-altitude treatments and high altitude on the right. Although there were no significant differences in final percent fruit removal between low and high altitude plants across all plants, there was a noticeable delay in fruit ripening for *G. depressa* at higher altitudes, particularly at Temple Basin (Figure 2.5). Higher numbers of unripe fruits were present on high-altitude plants than low-altitude plants in February at Cass (Figure 2.3 and 2.4), while unripe fruits were still abundant on high-altitude plants through until the first heavy snowfall in April at Temple Basin (Figure 2.5).

The highest instantaneous percentage of ripe fruits counted at any census was usually in February, except for high altitude *G. depressa* plants at Temple Basin. Of all treatments,

altitudinal levels, sites and years, the largest numbers of ripe and overripe fruits were on plants in cage and lizard-only cages at Temple Basin, suggesting that lizards played a negligible role in the removal of *G. depressa* fruits at that site.

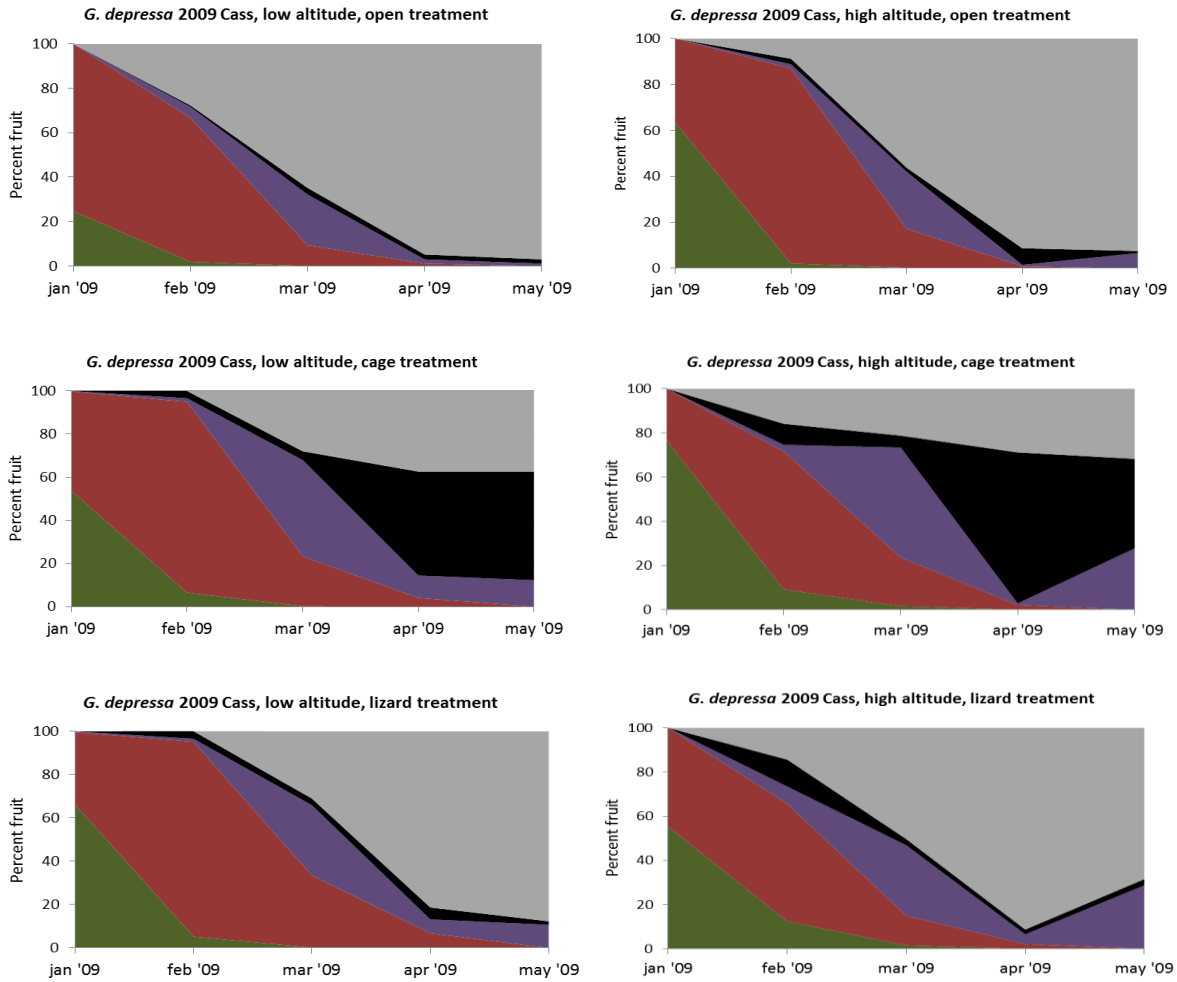


Figure 2.4 Fruit ripening and removal rates over time for *Gaultheria depressa* during the 2009 fruiting season at Cass for low (n=5) and high (n=5) altitude plants under open-access (n=5) and cage (n=5) and lizard-only (n=5) treatments. Total percentage of fruits in each category: green = unripe, red = ripe, purple = overripe, black = fallen, grey = gone.

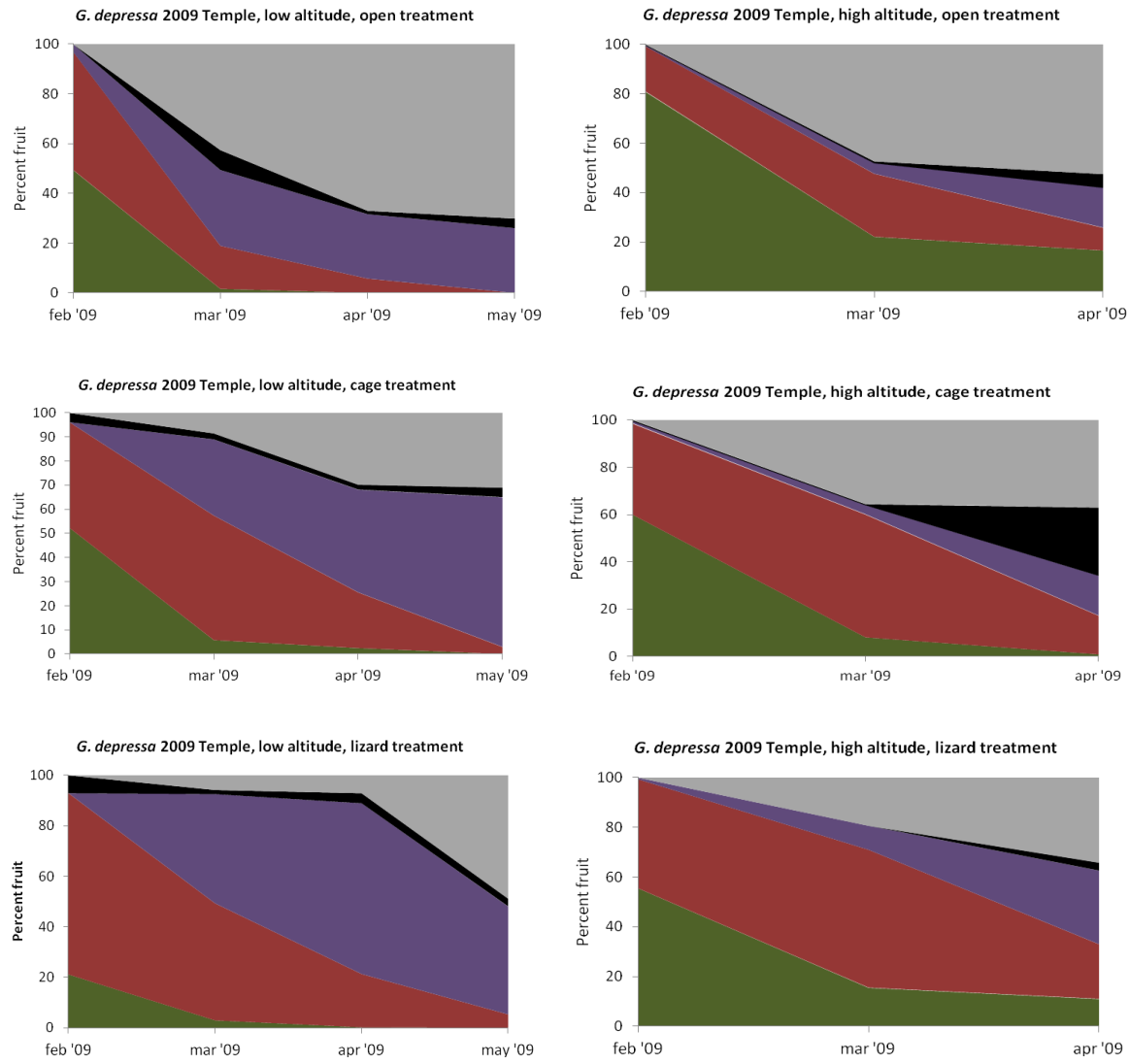


Figure 2.5 Fruit ripening and removal rates over time for *Gaultheria depressa* during the 2009 fruiting season at Temple Basin for low (n=5) and high (n=5) altitude plants under open-access (n=5) and cage (n=5) and lizard-only (n=5) treatments. Total percentage of fruits in each category: green = unripe, red = ripe, purple = overripe, black = fallen, grey = gone.

Fruit colour polymorphism, fruit ripening and removal in Leucopogon colensoi

Since there was no significant effect of year or altitude on final percent fruit removal at Cass (Table 2.2), these treatments were combined to present fruit ripening and removal over time for *L. colensoi* red versus white fruits (Figure 2.6). Mean final percent removal for red fruit in open-access treatments was 85% and 67% for white fruit in open-access treatments. This difference was not statistically significant (p = 0.26). The only significant

difference in mean percent fruit removal for colour treatment was in lizard-only cages, with higher mean percent removal for red fruit (67%) than white fruit (50%) ($p = 0.026$). There was no difference between red and white fruit removal in cage treatments.

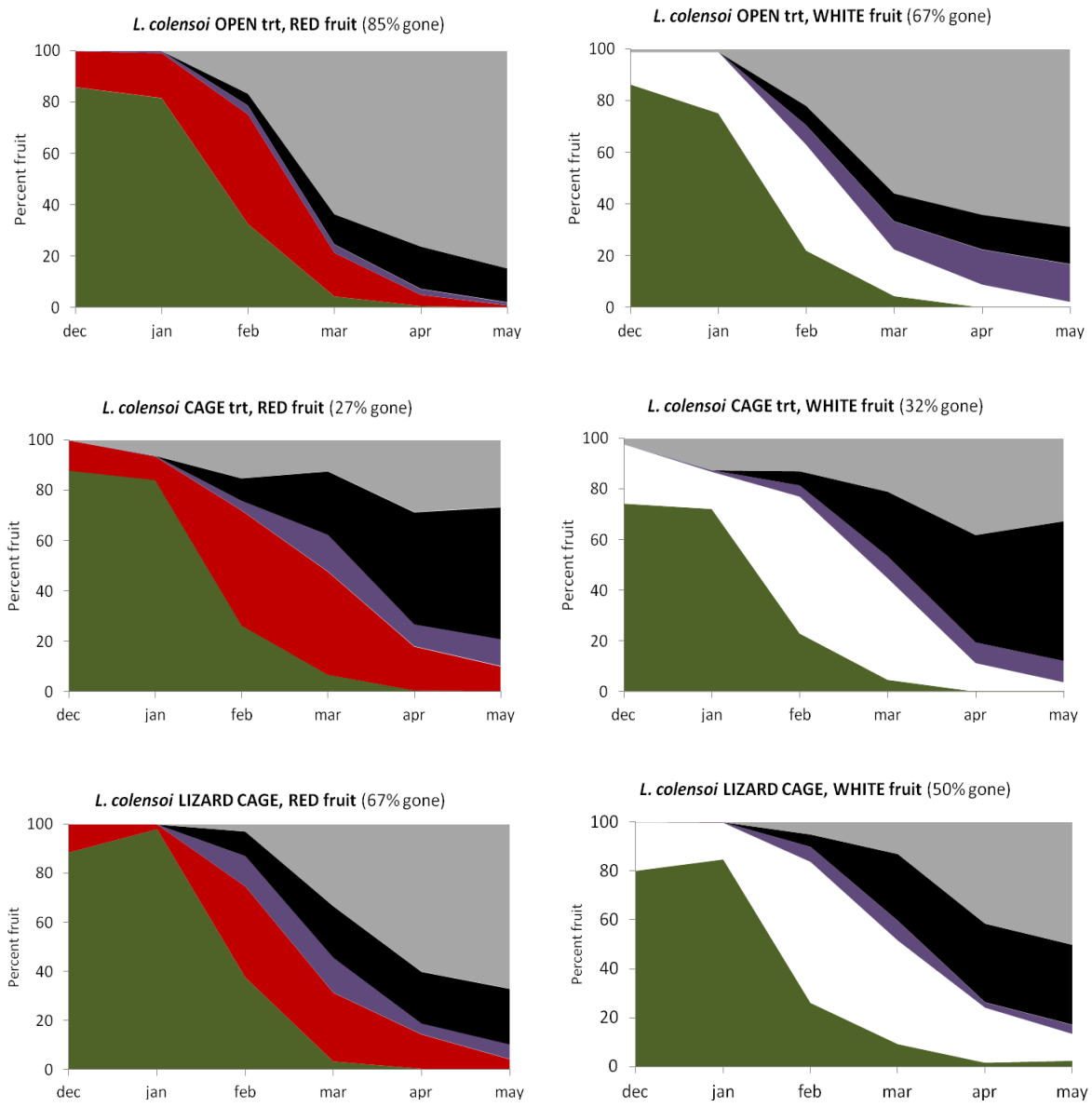


Figure 2.6 Fruit ripening and removal rates for *L. colensoi* in open-access (top graphs), cage (middle graphs) and lizard-cage (bottom graphs) treatments at Cass across both 2008/2009 and high/low altitude treatments combined. The effects of red and white fruit colour polymorphisms on fruit removal are shown by the colours in the "ripe" fruit category in red (graphs on left) and white (graphs on right) respectively. Total percentage of fruits in each category: green = unripe, red/white = ripe, purple = overripe, black = fallen, grey = gone.

Discussion

Is fruit removal adequate?

Fruit removal for these nine montane and alpine fleshy-fruited plants under the current suite of available native and exotic frugivores varied depending on species, with overall mean percent fruit removal ranging from 25-60% in open-access treatments, 21-33% in lizard-only treatments and 2-22% in animal-exclusion cage treatments across species (except *M. axillaris*, see below). Is fruit removal of these species high enough for adequate dispersal and how does this compare to fruit removal of other species or in other systems? The fruit removal rates in this study were probably nearer the low end of the range in the literature. Herrera (1984) found total removal rates of 89-100% for seven shrub species in Spain, while in Australia the shrub *Coprosma quadrifida* had 84% of fruits removed by 14 bird dispersers (French et al., 1992). In South Carolina USA, removal rates averaged 72% across 22 species (McCarty et al., 2002).

Very few New Zealand studies have monitored fruit fate over time to determine whether adequate levels of dispersal service are occurring (but see Kelly et al., 2004; Robertson et al., 2008). Kelly et al. (2004) monitored fruit ripening and removal over four years for two Loranthaceous mistletoes growing on host mountain beech (*Nothofagus solandri*) at nearby Craigieburn forest park, (20 km from Cass). For both *Alepis flavida* and *Peraxilla tetrapetala*, there was no evidence of dispersal limitation with very few (< 5%) fruits present on plants at any one time and > 90% of the total fruit crop removed. These were relatively high fruit removal rates in comparison to final percent fruit removal for most species in this study. For many species (see *G. depressa* and *L. colensoi* examples presented in results section above) there were often large numbers of ripe fruits present (20-70%) at any one time in open-access treatments, suggesting slow fruit removal and at comparatively lower levels than the mistletoes at Craigieburn. At Craigieburn, mistletoes are one of the only fruiting species available in the almost mono-specific mountain beech (*Nothofagus solandri* var. *cliffortioidies*) forest of the Canterbury foothills and mountains east of the Main Divide (Wardle, 1991; Murphy and Kelly, 2001). This suggests mistletoe fruits must be in high demand by bellbirds (*Anthornis melanura*) and other frugivorous forest birds, providing a highly important seasonal pulse of carbohydrate resource. Conversely, with so many fruiting species available in montane and alpine sites like Cass, there is more variety on offer, plus large quantities of fruit. Consequently, fruit removal of individual species could be lower.

Does this suggest dispersal limitation for certain alpine fleshy-fruited species? Robertson et al. (2008) propose that assessing whether fruit dispersal is inadequate is much harder than evaluating pollination limitation. They compared fruit removal rates on the New Zealand mainland with those on offshore Kapiti Island (a bird sanctuary with high bird densities) and found lower proportions of ripe and overripe fruits (0.9%) on uncaged branches at Kapiti than the mainland (up to 40%), suggesting rapid removal by birds. Both Kelly at al. (2004) and Robertson et al. (2008) suggest that as long as fruits are being removed at some point before they rot and fall below the parent plant, delays in fruit removal may have no fitness consequences. In this respect, mean final percent fruit removal by June (before winter snow cover settles) of greater 25-60% by any available seed disperser can thus be regarded as adequate.

Robertson et al. (2008) suggest that using the proportion of ripe or overripe fruit compared to green fruit may be used by managers as an approximate index of dispersal service to measure the level of mutualism service provided by native birds. However, because introduced mammals also consume large numbers of fruit, it is impossible to differentiate between whether birds or mammals are removing these fruit. Alternative methods should therefore be considered (Chapters 3 and 4) in order to more accurately evaluate the role of birds relative to other dispersers. Final percentage of the fruit crop removed and fruit removal rates depend on a variety of factors such as attractiveness (Willson and Whelan, 1990), conspicuousness (Lee et al., 1988), fruit crop size and neighbouring fruit crop availability (Blendinger and Villegas, 2011). Investigations into fruit removal should therefore consider these other factors when monitoring fruit fates to determine quantitative measures of seed dispersal effectiveness.

Fruit removal by lizards

The contribution by lizards to fruit removal was usually less than the contribution by other dispersers. This was not surprising, as cages with a mesh size large enough to only allow the entry of animals the size of geckoes, skinks and possibly invertebrate seed dispersers are obviously going to exclude most frugivores which would visit fruits on open-access treatment branches. In a separate but related study, I used lizard retreats (Artificial Cover Objects (ACO's)) to monitor: (a) which lizard species were present at the study sites; (b) their spatial distribution among different microsites in the landscape; and (c) their effectiveness as seed dispersers. I regularly monitored ACO's in three habitat types (grassland, rock/scree and shrubland) distributed along an increasing altitudinal gradient

(600-1700 m a.s.l.) at both sites. Results are intended for publication at a later date (after several more seasons of monitoring and faecal data collection) but preliminary findings suggest that the common skink and Southern Alps gecko are relatively widespread (but not particularly abundant) at Cass, while at Temple Basin I have never seen any evidence (in ACO's or otherwise) indicating the presence of lizards. Even if there are some present, they must be in very low numbers compared to at Cass. This could explain why there was very little difference in final fruit removal between lizard-only cages and animal-exclusion cages at Temple Basin (see *G. depressa* results in Figure 2.5). For the plants species studied at Cass, overall fruit removal levels were intermediate between cage and open-access treatments, suggesting that some fruit removal by lizards (and potentially smaller animals such as mice and invertebrates) was occurring.

Fruit colour polymorphisms and the variety of fruit colours in alpine plants

Here I do not attempt to answer evolutionary questions about the maintenance of fruit colour polymorphisms and their prevalence in the alpine flora, but simply investigate whether fruit removal differs depending on fruit colour in a common colour polymorphic species (*L. colensoi*) under varying disperser access scenarios. For open-access fruits there was no significant difference in final percent fruit removal between red and white fruited plants, although red fruits had slightly higher mean final percent fruit removal. Birds are reportedly more attracted to red fruits over light-coloured fruits (Willson and Whelan, 1990) and based on this we might expect higher fruit removal from red plants and perhaps selection for red fruits if birds were still the only available dispersers. However, with introduced mammals now part of the potential disperser fauna, this may explain the relatively equal levels of fruit removal between red and white fruited plants. Red fruited *L. colensoi* plants were considerably more common at the study site than white (pers. obs.), while dark pink, light pink and crimson coloured fruits were present at low densities. *Leucopogon colensoi* leaves are pale green-blue, often glaucous with a pinkish tinge especially in leaf buds and younger leaves, and to the human eye at least, red fruits were more conspicuous against their foliar background from afar.

The genus *Coprosma* (Rubiaecae) is one of the more speciose among New Zealand genera (ca. 53 species in New Zealand, Glenny et al., 2012), with a predominance of red-fruited species at higher altitudes, and many species with non-red fruits at lower altitudes (Lee et al., 1988). Lee et al. (1988) suggest that this phenomenon may be explained by the limited range of available dispersers and the brief period available for fruit removal before

winter snow. Many other common alpine species do possess red fruits (e.g., *P. nivalis*, *P. pumila*, *Lepidothamnus* spp.), but there are equally as many alpine taxa with non-red fruit colours (e.g., *Gaultheria* – white (sometimes pink), *Melicytus* – white/dark blotches, *Myrsine nummularia* – purple). The above reasoning cannot explain the prevalence of the large range of fruit colours present in the alpine zone. To explain the existence and maintenance of all these fruit colours would require larger studies testing multiple hypotheses and also test of genetic influences on fruit colour polymorphisms. However, further investigations could use the hypothesis suggested by Lee et al. (1988) using fruit colour-polymorphic species to test whether there are any relationships between fruit colour with increasing altitude. Additionally, studies using *C. propinqua* could investigate selection of different coloured fruits to see whether there are differences in frugivore taxa visiting purple/black, blue, yellow and white fruits and use germination experiments to determine whether there is a genetic basis for fruit colour polymorphism in this common montane *Coprosma* species.

In New Zealand, white fruits are relatively common, making up 21.2% of the 246 fleshy-fruited plants, while comparatively rare elsewhere in the world (Lee et al., 1988, 1994; Willson et al., 1989; Lord et al., 2002). New Zealand has an unusual and diverse array of seed dispersers, including mostly birds, lizards, invertebrates such as weta and grasshoppers and potentially bats. Because each of these taxa have different visual systems and activity periods, the unusual fruit colours present in the New Zealand flora may be a reflection of differential selection by different types of frugivores (Lord and Marshall 2001; Lord et al. 2002; Wotton 2002; Fadzly and Burns, 2010; Larsen and Burns 2012). Frugivore preferences among colour morphs are commonly found in laboratory choice tests (Willson, 1994; Puckey et al., 1996; Traveset and Willson, 1998), but are infrequently found in field studies of natural plant populations (Willson and O'Dowd, 1989; Whitney, 2005). Furthermore, the relative fitness of colour morphs has not been investigated in field settings even when feeding preferences by frugivores has been found. In general, very little is understood about the impacts of frugivores on the relative fitness of colour morphs and the maintenance of fruit colour polymorphisms globally (Whitney, 2005).

Species-specific traits and ecological peculiarities

Final fruit counts ceased for this study each year by June, (usually May, and for high altitude species at Temple Basin in 2009 – as early as April) because of snowfall which covers plants causing fruit counting to be impractical. The highest plants monitored at

Temple Basin were nearly 1700 m a.s.l. Many plant species with animal-dispersed fruits commonly grow at these altitudes across much of the South Island, but, because of snow cover which can persist until late spring/early summer and settle from late summer (Shanks et al., 1990), they have a relatively short season available to them to ripen and disseminate their fruits (Kudo, 1992). In this study I found that undispersed ripe fruits can remain on the plant over the winter months for some species (particularly *C. cotoneaster*, and less commonly in *C. propinqua*), available for frugivore consumption even after winter snow melt well into the following summer. This can happen while the next season's green fruit crop is developing and ripening. This is also the case for *Peraxilla tetrapetala* at Cragieburn, where some fruits ripen as late as January the next year (Kelly et al., 2004). Of all the study species, *C. cotoneaster* fruits were usually the slowest to be removed, with many shrubs bearing large quantities of ripe fruit late in autumn. This would suggest *C. cotoneaster* has one of the least-preferred fruits available among the montane and alpine flora studied. Its fruits are usually red but can be orange or yellow and have a seed enclosed inside a very large and hard endocarp (Webb and Simpson, 2001), more like a thin layer of skin surrounding the endocarp, which offers very little fruit pulp as a reward. It is thus not surprising that, even though abundant *C. cotoneaster* fruits are available, frugivores would prefer other species first and perhaps eat *C. cotoneaster* fruits later in the season once most other fruits have disappeared. One evolutionary explanation could also be that *C. cotoneaster* has lost one (or some) of its original dispersal agents. Fruits (particularly *C. cotoneaster* in mid-Canterbury) were abundant in the diets of extinct herbivorous moa (e.g., *Dinornis*) species (Burrows et al., 1981; Burrows, 1989), and Wood et al. (2008) found seeds of up to 30 different plant species in moa (*Dinornis*, *Pachyornis* and *Megalapteryx*) coprolites from central and west Otago. There has been a considerable amount of debate about the potential role of moa (especially via herbivory) in the evolution of a range of distinctive growth characteristics found across a taxonomically diverse range of New Zealand plants (e.g., unusual growth forms such as heteroblastly, divarication and mimicry) (Greenwood and Atkinson, 1977; McGlone and Webb, 1981; Atkinson and Greenwood, 1989; McGlone and Clarkson, 1993). Perhaps this could be further extended to co-evolutionary mutualisms such as seed dispersal. Seeds with hard endocarps are common in species that moa are known to have eaten (e.g., *Cyathodes*, *Leucopogon*, *Myrsine* and *Corokia* species). These types of theories can be investigated further by testing if these hard seed coats are an evolutionary adaptation to avoid damage after being eaten by moa or simply a phylogenetic trait. Using phylogenetic analyses we

might see a higher than expected proportion of species in the flora with hard endocarps or seed coats if they evolved in the presence of moa. Wood et al. (2002) suggest that moa are likely to have played a major role in seed dispersal of a range of plants, and some evidence for dispersal loss in several endangered species of dryland 'spring annual' herbs exists (Rogers et al., 2002). With the increasing amount of evidence on the diets of extinct (or functionally extinct) megaherbivores in New Zealand (e.g., Burrows et al., 1981, Horrocks et al., 2004, 2008; Wood et al., 2008) we are able to start painting a picture of past mutualisms and relate this to modern-day ecosystem functioning.

Another intriguing phenomenon I observed during this study is the back-up dispersal mechanism used by *G. depressa* if fruits were not removed by a frugivore or did not fall off the parent plant. Most fruits in open-access plants were removed eventually, while in animal-exclusion cages many fruits remained attached, particularly at Temple Basin. During the 'overripe' stage, fruit pulp shrivelled and dried up, exposing the internal seed-containing capsule. In fruits inside cages, I noticed that these tiny seeds were being dispersed by exiting the capsule with each wind gust. To my knowledge, this "plan B" for effective dispersal of *G. depressa* has not been reported in the literature. Other New Zealand *Gaultheria* species have dry capsules containing hundreds of tiny seeds, while others are fleshy-fruited (technically with swollen calyx enclosing the dry capsule), presumably adapted for frugivorous seed dispersal. Further study can confirm whether this back-up mechanism for dispersal is common, widespread or unusual for other *Gaultheria* species as well as other unrelated taxa.

This study has not only provided some important detail on the current overall effectiveness of fruit removal for several montane and alpine fleshy-fruited plant species, but also some basic information on fruiting phenology and ecological peculiarities of some of these species. With the knowledge that fruits are being removed in more or less adequate (but not high) levels for these species, the next step is to determine who the frugivores are, their post-dispersal effects on seeds such as deposition into appropriate microsites and effects of gut passage on germination, growth and survival.

APPENDIX A2.1 Some problems encountered while working with these plants

Although results suggest that *P. nivalis* fruits also have relatively low fruit removal overall, some of this is probably due to the uncertainty in counts of green fruit during monthly censuses and whether green fruits are part of the current year's fruit crop or the following. Podocarp fruits are thought to produce and develop the seed crop during one year and ripen the fruits (technically a swollen fleshy receptacle) over the following season (Beveridge, 1965). However, although this appeared to be the case at Cass, it was possibly not true for Temple Basin *P. nivalis* plants. During the only study season at Temple Basin (2009) either: no seeds were produced and waiting to be developed the following season (unlikely because of the abundance of tiny developing seeds covering plants), or there is no strict rule of thumb for the production and ripening of seeds across two seasons. Fruits seemed to ripen all through the season and were even present during mid-winter, apparently from these tiny immature seeds. Perhaps there is less of a two year effect of fruit crop ripening in *P. nivalis* then, and more of a slow and steady ripening of fruits across the year regardless of season, and this could also be dependent on site and altitude. If this was the case, it could might confer a selective advantage to these plants, (especially at higher altitudes where there are no other fruiting species available for potential dispersers like kea and other alpine birds over winter), in ensuring some fruits are available for hungry frugivorous animals and can be dispersed year-round. This would be an interesting avenue for further investigation, particularly comparing different populations of these plants at their upper and lower altitudinal ranges. *Podocarpus nivalis* grows high up into the alpine zone (to >1500 m a.s.l.) (Mark and Adams, 1995), higher than most of the other species in this study, and probably offers one of the only fruit sources during the harsh alpine winter months.

Some species were extremely difficult to work with, particularly *M. axillaris*. Flowers were constantly being produced over at least four to five months, many developed fruits but many were aborted and dropped off. This made keeping track of fruit fates over time very difficult because new fruit were always appearing at each census. Moreover, fruits of *M. axillaris* had the propensity to fall off even with any gentle touch, making it nearly impossible to accurately monitor fruit fates. Therefore, the effectiveness of fruit removal cannot be easily assessed for this species (as implied by the apparent high percent fruit removal from inside cages) and more work is needed if we are to determine whether *M. axillaris* is dispersal limited.

CHAPTER THREE

The importance of introduced mammals in dispersing alpine plants

Mostly intact seeds of *Podocarpus nivalis* dispersed via faecal matter onto scree. (Photo: L.M. Young)

Abstract

Seed dispersal by animals is a key process in shaping plant communities, yet there is increasing concern about the potential effects of changing frugivore communities on ecosystems and individual plant species. In New Zealand, fleshy-fruitedness is prevalent in the indigenous alpine flora yet the native disperser fauna (birds and lizards) have declined greatly since human settlement. Using a community-level approach, I investigated the roles of the exotic mammalian fauna in seed dispersal of the alpine fleshy-fruited flora. Fixed-area plots covering 3000 m^2 and representing a range of montane to alpine vegetation types (shrub, open grassland, mat and herbfield and rocky scree) were monitored regularly by counting and clearing all animal pellets over two fruiting seasons at two sites in the central Southern Alps, New Zealand. The relative abundance of mammal species was assessed and spatial patterns of faecal deposition were examined in relation to dominant habitat (and subsequent germination sites). Faecal analyses revealed large quantities of fruits eaten, particularly by small mammals (possums, lagomorphs and hedgehogs). Seeds from 67 plant species were found in the faecal samples, with high quantities of these from fleshy-fruited alpine plants. There were very low levels of seed predation, with most animals dispersing >95% of seeds intact. Sheep faeces were found in the highest densities (> 7.9 m^2 yr^{-1}), followed by lagomorphs (6 m^2 yr^{-1}) then possums (> 1.5 m^2 yr^{-1}). Possums faeces had more seeds per pellet, and dispersed the most seeds (> 160 m^2 yr^{-1}), relative to sheep and lagomorphs which each moved roughly 50 seeds m^2 yr^{-1}. At Cass, possums largely dispersed seeds into forested habitats which are unsuitable for regeneration of most alpine plant species, while sheep and lagomorphs dispersed most seeds to open grassland. Few faeces were found from rodents, birds, lizards and invertebrates, but the sampling method probably underestimates their contributions. These results show that, in mountain habitats, introduced mammals are dispersing large numbers of seeds (dispersal quantity), perhaps partially replacing absent native birds and lizards. However, mammals may be dispersing seed to unsuitable microsites and limited distances, especially compared to the native kea. Exotic mammals also have detrimental impacts on native flora directly (through herbivory) and indirectly (through predation on native dispersers).

Introduction

Seed dispersal by animals is an essential service to plants and a key process in shaping plant communities (Nathan and Muller-Landau, 2000). A worldwide decline in frugivorous animals has generated increasing interest in understanding the effects of disperser loss on plants (Bond, 1994; Guimares Jr. et al., 2008). Several studies have demonstrated negative impacts on seedling recruitment and plant regeneration through loss of their seed dispersers (e.g. Christian 2001; McConkey and Drake 2002; Traveset and Riera 2005; Sharam et al., 2009; Wotton and Kelly 2011). Frugivore decline is likely to be of more conservation concern on oceanic islands than continental ecosystems because islands harbour fewer species of frugivorous vertebrates than comparable mainland areas (Hansen et al., 2008). On numerous islands, many seed dispersal interactions are likely to have been lost because extinct frugivores currently outnumber the living (Hansen et al., 2008). With many areas now dominated by introduced species, there is a growing body of research investigating whether introduced animals can function as effective seed dispersers and act to replace or compensate in areas where the original disperser fauna is now depauperate (e.g. Janzen and Martin, 1982; Hansen et al., 2008; Staddon et al., 2010).

New Zealand, like numerous other islands, has lost the majority of its "megafauna" (*sensu* Hansen and Galetti, 2009) (using a context-dependent definition of megafauna – "in any given ecosystem, the largest vertebrates have ecosystem impacts that are similar on a relative scale to those of the largest vertebrates in another ecosystem"). On continents the extinctions of classic mammalian megafauna such as gomphotheres and ground sloths, and on islands the loss of large birds and reptiles, have disrupted seed dispersal mutualisms for large fruits (Janzen and Martin, 1982; Guimares Jr. et al., 2008). Wotton and Kelly (2011) have demonstrated similar effects in New Zealand, with declines in the largest remaining frugivorous forest bird (New Zealand pigeon, *Hemiphaga novaeseelandiae*) leading to reduced dispersal and consequently reduced regeneration for two of the largest-seeded trees in New Zealand forests.

To better understand the role of seed dispersal in maintaining biodiversity, it is essential to analyse animal-fruit interactions at the community level, i.e. considering all species at a given locality (Chapman and Chapman, 1995) and their relative effectiveness. Seed dispersal has quantitative and qualitative aspects (Schupp, 1993) and frugivores may differ in the effectiveness of their contributions to both. Quantity of seed dispersal depends

on the number of visits a disperser makes to a plant, and the numbers of seeds dispersed per visit, while dispersal quality depends on seed treatment (in the mouth/beak and gut) and the seed deposition site (Schupp, 1993). By studying seed dispersal effectiveness at the community level, overall impacts of changes in the frugivore community can be determined.

Seed dispersal in New Zealand has largely been studied in forest communities and for larger-seeded plants (e.g., Williams and Karl, 1996; Anderson et al., 2006; Wotton and Kelly, 2011), for it is these in particular that are deemed most at risk due to the loss of large avian frugivores (Clout and Hay, 1989). However, seed dispersal is particularly important in naturally fragmented ecosystems, such as mountain tops where the alpine areas are analogous to islands surrounded by 'seas' of forest. Dispersal of seeds between alpine areas is essential for maintaining genetic connectivity between patches, metapopulation persistence, and long-term species survival (Nathan and Muller-Landau, 2000). In New Zealand's alpine areas, which constitute around 13% of the total land area, little is known about animal-plant dispersal mutualisms. Fleshy-fruitedness is relatively common (12% of species) in the New Zealand indigenous alpine flora compared to other temperate alpine plant communities. For example, fleshy-fruited species represent only 3-5% of the alpine flora in Victoria, Australia and 5.4% in Chile (Lord, 1999 and references therein). However, despite the prevalence of fleshy-fruited alpine species in New Zealand, there are few extant native frugivores to disperse the seeds.

Birds and lizards were the dominant fauna in mountain ecosystems, until terrestrial vertebrate communities in New Zealand drastically changed (Tennyson, 2010) after the arrival of humans in ca. 1280 AD (Wilmshurst et al., 2008) and the associated introduction of mammalian pests (including ungulates, rodents, mustelids and lagomorphs). Native birds and lizards have declined, but some exotic birds and mammals – now abundant and widespread – are potentially important seed dispersers (Bell, 1991; Kelly et al., 2010). Little is known about what effects this defaunation has had on the plants, and until recently little was known about alpine seed dispersal by the native frugivorous avifauna (Young et al., 2012; Chapter 4). If introduced mammals are capable of effective seed dispersal in New Zealand's alpine zone, then concerns about the paucity of native disperser fauna could be alleviated. However, any benefits provided by the exotic dispersers might be offset by costs such as herbivory, competition with, and predation on, remaining native frugivores.

To determine the seed dispersal effectiveness of distinct dispersal agents, disperser behaviour needs to be linked with spatially explicit patterns of seed arrival (Schupp et al.,

2010). This is an important part of the seed dispersal process because it ultimately determines whether the plant has any chance of germinating and surviving to reproductive age – the true definition of successful seed dispersal. A recent review (Schupp et al., 2010) has highlighted a shortage of studies that directly link dispersal agent activity with the actual seed rain reaching specific microhabitats.

The aim of this study was to investigate the seed dispersal effectiveness of exotic mammals in alpine fruit dispersal in New Zealand, including seed deposition site. Specific objectives were: 1) to determine which animals are dispersing seeds of fleshy-fruited alpine plants; 2) to record the relative contributions of various mammals to seed dispersal of fleshy-fruited native alpine plants (dispersal quantity); 3) to determine the proportion of seeds dispersed intact vs. in fragments after handling and gut-passage (one aspect of dispersal quality); and 4) to establish the microhabitats to which seeds are being dispersed by mammals.

Methods

Study sites and species

Field work was conducted at two sites: Cass (43^{o} 2' S, 171 ^{o} 47' E), 5 km east of the Arthurs Pass National Park eastern boundary, and Temple Basin (42^{o} 54' S, 171^{o} 34' E), within Arthurs Pass National Park, both in the Canterbury region, South Island, New Zealand. Both sites are characterised by areas of open high-country grassland, mixed scrub/shrub, herbaceous and mat plants interspersed with scree and rock. Similar habitat also occurs at lower (montane) altitudes as low as 650 m a.s.l., where burning has lowered the treeline (but small forest patches remain). At least 50 native fleshy-fruited plant species within 24 genera and 14 families occurred at the sites. All fruits contained small seeds 0.4 to 6.0 mm length (see Appendix A1 in Young et al., 2012, Chapter 4).

The study sites typify two montane-alpine land management levels, important in understanding whether differences in disperser fauna between these areas affect seed dispersal processes. Between-site differences include the land's conservation status and subsequently, differences in the animal fauna. Temple Basin is typical of conservation land under National Park status while Cass represents non-conservation, low intensity grazed land (see Burrows, 1977). Exotic mammals including Australian brushtail possums (*Trichosurus vulpecula*), European hares (*Lepus europaeus*) and rabbits (*Oryctolagus cuniculus*), and

chamois (*Rupicapra rupicapra*) are present at both sites while Cass also has frequent domestic sheep (*Ovis aries*), hedgehogs (*Erinaceus europaeus*), stoats (*Mustela erminea*), feral cats (*Felis catus*), ship rats (*Rattus rattus*), house mice (*Mus musculus*), and occasional pigs (*Sus scrofa*) and red deer (*Cervus elaphus scoticus*). Two lizard species, approximately 10 native and 12 introduced bird species are present at both sites, of which the kea or mountain parrot (*Nestor notabilis*), and pipit (*Anthus novaeseelandiae*) are the most important dispersers (Young et al., 2012; Chapter 4).

Seed dispersal patterns through faecal transect sampling

I used fixed-area faecal transects to: (1) quantify numbers of seeds excreted (intact and in fragments) in faeces by different animals; (2) determine which habitats seeds are moved to by all dispersers; and (3) estimate the relative abundance of animals from faecal density. Faecal transects were positioned across six subsites that differed from each other broadly, principally by altitude (650 m to 1650 m a.s.l.) and subsequently vegetation composition, geology and slope. Four distinct subsites were identified at Cass, and two at Temple Basin. Within these subsites, fixed-area transects 30 m in length were selected in a stratified-random fashion, where the strata were habitat type (forest, shrubland and grassland). All transects ran across-slope, and were subdivided into thirty contiguous 1 x 1 m subplots either side of the fixed transect line, totalling 60 m^2 for each transect. I monitored 30 transects at Cass and 20 at Temple Basin, providing a total sampling area of 3000 m^2. Each 1 m^2 subplot was visually assessed for vegetation cover and allocated to one of four broad habitat categories based on its dominant cover: 1. beech forest, 2. shrub (≥ 60% shrub cover), 3. open (≥ 60% grass/mat/herb/bare ground < 30 cm tall), or 4. mixed open-shrub (40-60% open and shrub). Percentage of open vegetation (see definition above) was also calculated in each subplot, (i.e. all (non-shrubby) vegetation with the potential for mammals to move through). I also recorded the presence of each fruiting species (fruit-bearing individuals only) and animal pathways within each subplot.

Transects were set up during January and February 2009 and all faeces were cleared from the subplots at that time. I then collected faeces deposited over the next 16 months, covering two fruiting seasons (2009 and 2010). Between February 2009 and May 2010 all subplots on each transect were sampled five times at Cass and four times at Temple Basin. All new animal faecal pellets were counted and collected. I used samples from known species previously collected from the study area by C.J. Burrows to compare faeces against for

identification, along with information from P. Sweetapple at Landcare Research, Lincoln and notes in King (2005). With the exception of hare and rabbit pellets which were grouped for analyses and referred to as lagomorphs, most faeces were readily identifiable to species because of distinct differences in size and shape between the different animals.

Faecal analysis, seed identification and seed viability

Faeces were dissected in order to find and identify any seeds within them, using a stratified subsampling method. For subplots containing fewer than ten faeces per animal species, all faeces were dissected. For subplots with > 10 faeces, I dissected between 10 and 20 faeces per animal species, per subplot, per collection period (i.e., a maximum of 100 faeces from any given subplot across the 16 month sampling period). In total, nearly 10% (2,338) of all collected faecal samples (25,537) were analysed for seeds. A dissection microscope (6–40 x magnification) was used to find and identify seeds. Seeds were sorted from each faecal sample for each animal species into intact and fragmented bits. Counts of seed fragments presented in the results are likely to provide an overestimate of the true proportion of destroyed seeds because a single shattered seed creates multiple fragments. Samples of all seed species were classified according to the animal faeces they were found in. Intact seeds of the most common species were tested for viability by sowing them in potting mix in trays inside an unheated glasshouse and then counting seedling emergence over the following three years. All analyses presented here are numbers of seeds unless otherwise specified.

Recording frugivores using infra-red video technology

I also identified animals eating fruits using a Swann DVR4-1000 battery-powered digital video recorder with four infra-red cameras monitoring fruiting plants. The camera system was set up at Cass. Filming took place during both day and night. The cameras ran at each site usually for at least a full 24 hour period before relocating them to a different area. Five separate areas (covering a subset of the study plant species) were filmed during the 2010 fruiting season, giving a total of 425 hours of surveillance. I watched all video footage and obtained qualitative data on the occurrence of animal visits to plants and whether fruit was eaten.

Statistical Analysis

Bipartite Interaction Networks

I used a quantitative weighted bipartite interaction network to depict plant-disperser interactions and the relative strength of these interactions. Rather than presenting data on the total numbers of seeds dispersed by each animal species, I calculated the number of dispersal units (or diaspores) consumed, using the average number of seeds per fruit. Most of the sampled plant species have 1 or 2 seeds per fruit, but a few (particularly *Gaultheria* species) have hundreds of seeds per fruit, so an analysis at the seed level would be dominated by *Gaultheria*. Using the plotweb function in the *bipartite* package (Dormann et al., 2008) for the statistical package R (R Development Core Team, 2011), which focuses on interaction webs for two trophic levels, I created a community dispersal web for all plants and animals based on faeces data collected over 16 months.

Animal faecal distribution

Using the Information-Theoretic Model Comparison (ITMC) approach (Burnham and Anderson, 2002), I modelled the distribution of faeces across the landscape separately for each animal species using a two-stage analysis. I used generalised linear mixed effects models (GLMMs) which allowed both fixed and random effects to be incorporated in the models. The Information Theoretic approach is favoured because a small number of ecologically relevant variables are defined *a priori* using knowledge of the study system (Burnham and Anderson, 2002). This approach is highly recommended for making formal model inferences and can provide more meaningful model likelihoods and probabilities using Akaike's Information Criteria (AIC) (Anderson, 2008). I employed the multi-stage analysis approach to deal with the issue of having data that contain both a substantial proportion of zeros and are positively skewed (common issues in ecological animal abundance data (Fletcher et al., 2005)). Models were developed using the R statistical programme (R Development Core Team, 2011) with the packages *lme4* (Bates et al., 2011) and *AICmodavg* (Mazerolle, 2009).

I created two separate datasets from the original. One had the faecal presence/absence data of the response variable (presence of faeces m^2 yr^{-1} for each animal), called "presence" data, and was analysed with a binomial error distribution in generalised linear mixed effects models (glmer function). The other had the non-zero counts when faeces were present (faeces

m^2 yr^{-1}), called "abundance" data, and was analysed with a poisson error distribution with linear mixed effects models (lmer function). Presence data were analysed only for species with sufficient plots with faeces present (lagomorphs, possums, sheep, hedgehogs and pigs), and analysed separately by site (because of the absence of some species from Temple Basin). Abundance data were analysed for the three most abundant taxa, lagomorphs, possums and sheep.

Measured predictor variables

Two separate habitat measures were used in the models. (1) Dominant habitat (DH) was a four-level factor variable comprising forest, shrub, open or mixed (40-60% open and shrub) cover; and (2) proportion of open vegetation cover (OV). Dominant habitat and proportion of open vegetation were never included together within a model due to their collinearity. Two fruit availability measures were included in the models: a binary variable for the presence of *any* fruiting species (Fp) in a plot, and the number of fruiting species (Fn) in a plot. The presence of animal pathways (AP) through a subplot was noted in the field and incorporated into models as a binary predictor variable (pathways present or absent).

Model selection with the Information Theoretic approach

The above measured variables were specified as fixed effects in the models, while the nesting of subplots within transects and transects within subsites were specified as random effects. Cass and Temple Basin sites were analysed separately because of the differing number of times each site was resampled over the 16 months (5 and 4 respectively).

Using the predictor variables specified above, an *a priori* set of 14 candidate models (i.e. 14 alternative hypotheses) was formulated, plus single-predictor and random effects-only models (see Appendix 2 for the full set of models). Random effects models allow separate estimation of a component of variance due to sampling or study design separate from a process variance component (e.g. spatial variation caused by transect effects rather than habitat variation). Below are the global models for the presence and abundance data respectively.

Faeces presence ~ DH or OV + Fp + Fn + AT, (1 | transect:subsite), family = binomial

Faeces abundance ~ DH or OV + Fp + Fn + AT, (1 | transect:subsite), family = poisson

Multimodel inference

Model selection based on Akaike's Information Criteria (AICc for second order bias correction) was conducted on the set of 14 candidate models, using identical models for the presence and abundance datasets. Log likelihoods and AICc values were estimated using the *lme4* package (Bates et al., 2011). For each model in the set, AICc was calculated and each model was ranked by rescaling the AICc values. The most parsimonious model was the one with the minimum AICc value and had a ΔAICc value of 0, i.e. $\Delta_i = AICc_i - AICc_{min}$ which estimates the expected distance between the best model and the $_i^{th}$ model. Models for which $\Delta_i \leq 2$ are considered to have substantial support, while models with $\Delta_i \geq$ 10-12 essentially have no empirical support (Burnham and Anderson, 2002). To compare models, Akaike weights (W_i) (normalised likelihood models) were calculated so that values for all models sum to 1. Akaike weights provide an approximate probability for model *i* being the best model and are an ideal way of examining the relative strength of evidence for each model within the set. The higher the value, the more weight is put on the associated model in comparison with the others. Cumulative Akaike weights ($Cum.w_i$) were calculated and models with a $Cum.w_i \geq 0.95$ are presented in the results as a set of confidence models. Goodness of fit of the models was evaluated using an adjusted R^2 calculation and these R^2 values are presented for the top model in each set. Parameter estimates (using Laplace approximations) of regression coefficients and unconditional standard errors which incorporate a variance component due to model selection uncertainty, (Burnham and Anderson, 2002) were calculated and are presented for each predictor variable present in the top model for each set (Appendix A3.4).

Results

A total of 25,537 faeces was collected from eleven animal taxa, including eight mammalian species, across the 16 month sampling period. In the 2,338 faeces (ca. 10%) that were dissected for seeds, 90,760 intact seeds from 67 plant species were recorded (Table 3.1 and Appendix 3.1). The majority of seeds dispersed were from fleshy-fruited montane, subalpine and alpine plants, with few weedy species present (see Appendix Table A3.1 for full plant species list). Sheep produced the highest densities of faeces but excreted fewer seeds (ca. 60 seeds m^2 yr^{-1}) compared with possums which produced only one-fifth as many faeces while dispersing nearly three times as many intact seeds (ca. 160 seeds m^2 yr^{-1}). Lagomorphs produced high numbers of faeces and dispersed approximately 50 seeds m^2 yr^{-1} intact. Other animals produced much lower numbers of faeces (Table 3.1, and Figure 3.1) but some of these, particularly hedgehogs and pigs, nonetheless made a notable contribution to seed dispersal quantity. Bird faeces were rarely found, but this is possibly an artefact of the sampling method (see below).

Table 3.1 Summary statistics for mammals and other animal taxa at Cass and Temple Basin combined showing percent of subplots with faeces present, total numbers of faeces collected, number of faeces subsampled, numbers of intact seeds and species found within faeces and seeds moved by each animal $m^{2\ -1}$ yr^{-1}. The final column shows the percent of total seeds dispersed by each animal (column 5) out of all seeds dispersed (using raw faecal count data).

	% plots with faeces	Total faeces	Faeces $m^{2\ -1}$ yr^{-1}	Faeces sub-sampled	Total intact seeds	Mean seeds/ sample	No. seed species	Seeds dispersed $m^{2\ -1}$ yr^{-1}	% of all seeds moved
Sheep	7.7	12,966	7.900	300	2,258	7.5	25	60.24	2.45
Lagomorphs	42.6	9,619	5.900	1,263	11,454	9.6	18	54.38	12.68
Possum	10.3	2,488	1.500	671	70,996	105.8	37	162.50	78.24
Deer	0.03	106	0.065	11	36	3.3	1	0.21	0.04
Chamois	0.3	61	0.037	10	147	14.7	2	0.55	0.16
Pig	0.5	45	0.028	16	1,969	123.1	7	3.42	2.15
Hedgehog	1.0	37	0.020	37	2,938	79.4	10	1.81	3.17
Kea	0.2	15	0.009	12	665	54.6	9	0.51	0.74
Other birds	0.2	86	0.053	39	283	7.3	11	0.39	0.33
Lizard	0.1	3	0.002	3	0	0	0	0	0
Grasshopper	0.03	2	0.001	1	14	14	1	0.02	0.03
Totals		25,537		2,338	90,760		(67)	284.03	100

Lagomorph faeces were the most widely spread, with nearly 43% of subplots containing faeces on at least one occasion across the sampling period (Table 3.1). Although

sheep faeces were present in the highest densities, they were concentrated among a smaller portion of subplots. Possum faeces were also relatively common, while faeces from most other animals were each found in less than 2% of the subplots (Table 3.1).

The abundance of faeces remained relatively constant throughout the year for most mammals (Figure 3.1). Sheep were the exception to this pattern, with numbers increasing over the winter months and peaking in early summer 2009, coinciding with the herding of sheep into the Cass Scientific Reserve for winter grazing. Hedgehogs, pigs, deer and chamois were present at low numbers (Figure 3.1) and only appeared in sampling transects a few times each.

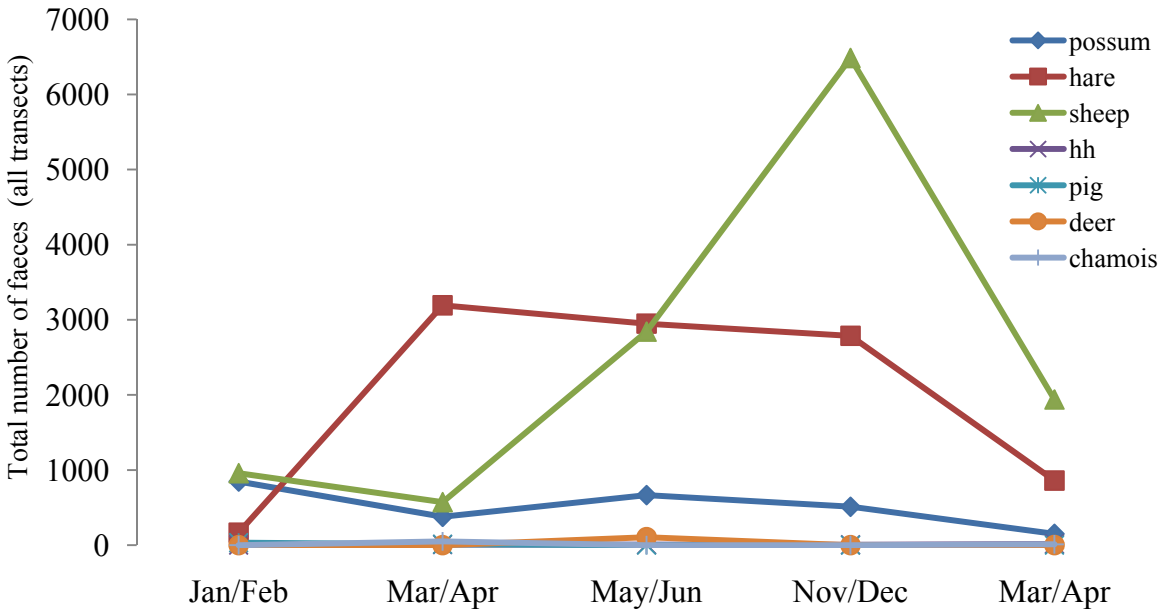


Figure 3.1 Variation in the total number of faeces for each mammalian species across the 16 month sampling period February 2009 to May 2010. (Note: hh in the legend refers to hedgehog).

Quality of seed dispersal (in relation to seed damage) was high among all animals, with each species dispersing ≥ 90% of ingested seeds intact (Appendix Table A3.2). However, there was large variation in the quantity of seeds dispersed by the various animals, with possums moving 78% of all dispersed seeds. Of the seeds dispersed by possums, 97% were dispersed intact (Table 3.1). Lagomorphs dispersed ca. 12% of all seeds, while all other animals each dispersed 3% or less of all seeds (Table 3.1).

Possums played by far the largest quantitative role in dispersal, both in the number of different species and the quantity of fruits dispersed (Figure 3.2). In particular, the majority of *Coriaria* species (CS and CPL), and *Gaultheria depressa* (GD) fruits were dispersed by possums, as well as smaller quantities of nearly all other plant species. *Leucopogon colensoi* (LC) fruits were moved in relatively large quantities and their dispersal was performed more or less equally by possums, lagomorphs and hedgehogs (Figure 3.2). Sheep dispersed seeds of many different plant species, but most of these were either one-off or rare events. Chamois and deer faeces were present in very low numbers (Table 3.1), probably reflecting the relative rarity of animals at these sites, so it is difficult to draw any firm conclusions about fruit species eaten and their importance for seed dispersal (Figure 3.2). Grasshopper, kea and "other bird" faeces were difficult to detect due to their small size, again meaning it is hard to draw conclusions about the role of those animals relative to mammals (but see Young et al., 2012 and Chapter 4).

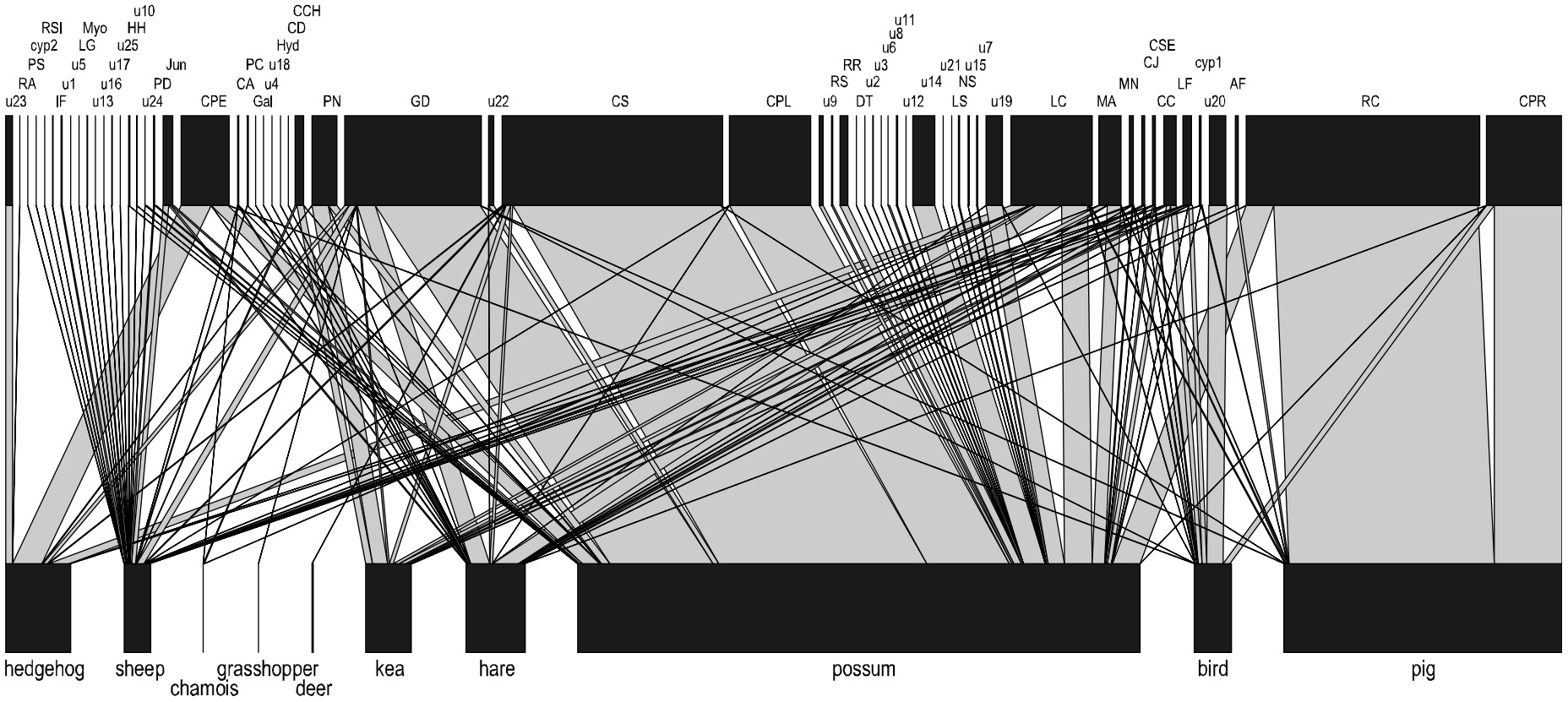


Figure 3.2 Bipartite interaction seed dispersal web showing community-level dispersal patterns for all fruit dispersed (top row) by all animals (bottom row) at Cass and Temple Basin over 16 months. The links between the bars represent an association between the plant and animal, while the variable thickness of the bars indicates the relative frequency of the interaction. The diaspore is the unit presented here (using mean number of seeds per fruit) as an ecologically relevant dispersal unit rather than the number of individual seeds dispersed. See Appendix Table A3.1 for full species list, but abbreviations for dominant species are (from left to right): CPE = *Coprosma petriei*, PN = *Podocarpus nivalis*, GD = *Gaultheria depressa*, CS = *Coriaria sarmentosa*, CPL = *Coriaria plumosa*, LC = *Leucopogon colensoi*, MA = *Muehlenbeckia axillaris*, RC = *Rubus cissoidies* and CPR = *Coprosma propinqua*.

Table 3.2 Summary results for the selected top models used to explain the **presence** of faeces for each animal type at both sites: Cass and Temple Basin. A set of 14 *a priori* (linear mixed effects) models was formulated and the best models were selected based upon the Akaike Information Criterion (AICc), with the top models having a cumulative Akaike weight (Cum. wi) ≥ 0.95 to make up a 95% confidence set. Model terms presented below show all fixed effects predictors only (but random effects (transect/site) are included in all models). Adjusted R^2 are presented for the best model only. Abbreviations for the predictors are: OV = proportion of open vegetation; DH = dominant habitat; AP = animal pathways; Fp = presence of fruiting species; Fn = number of fruiting species.

Species / Site	Model (Adj R^2)	K[a]	log($\mathcal{L}$)[b]	AICc	Δi [c]	Wi [d]	Cum.wi
Lagomorph / Cass	OV + Fp + AP (0.36)	5	-790.4	1590.9	0.00	0.29	0.29
	OV + AP	4	-791.8	1591.6	0.78	0.20	0.49
	OV + Fp	4	-792.0	1592.1	1.20	0.16	0.65
	OV + Fp + Fn + AP	6	-790.4	1592.9	2.00	0.11	0.75
	OV	3	-793.4	1592.9	2.03	0.11	0.86
	DH + AP	6	-791.1	1594.3	3.41	0.05	0.91
	DH + Fp + AP	5	-790.4	1594.9	4.08	0.04	0.95
Lagomorph / Temple	OV (0.33)	3	-636.9	1279.8	0.00	0.50	0.50
	OV + Fp	4	-636.8	1281.6	1.88	0.19	0.69
	OV + AP	4	-636.9	1281.8	2.01	0.18	0.87
	OV + Fp + AP	5	-636.8	1283.7	3.89	0.07	0.94
	OV + Fp + Fn + AP	6	-636.8	1285.6	5.85	0.03	0.97
Possum / Cass	DH + Fp (0.28)	6	-614.1	1240.2	0.00	0.41	0.41
	DH	5	-615.7	1241.4	1.18	0.23	0.64
	DH + Fp + AP	7	-613.8	1241.8	1.53	0.19	0.83
	DH + AP	6	-615.5	1243.0	2.77	0.10	0.93
	DH + Fp + Fn + AP	8	-613.8	1243.7	3.50	0.07	0.99
Sheep / Cass	Random effects (0.61)	2	-298.9	601.9	0.00	0.47	0.47
	Fn	3	-299.1	604.1	2.27	0.15	0.62
	OV + AP	4	-298.2	604.5	2.60	0.13	0.74
	Fp	3	-299.4	604.9	2.97	0.11	0.85
	DH + AP	6	-296.9	605.9	3.99	0.06	0.91
	DH + Fp	6	-297.6	607.3	5.39	0.03	0.95
Hedgehog / Cass	DH (0.03)	5	-137.2	284.5	0.00	0.34	0.34
	DH + AP	6	-137.1	286.2	1.72	0.14	0.49
	DH + Fp	6	-137.2	286.4	1.90	0.13	0.62
	Random effects	2	-141.6	287.3	2.82	0.08	0.70
	DH + Fp + AP	7	-137.0	288.1	3.62	0.06	0.76
	OV	3	-141.1	288.1	3.67	0.05	0.81
	Fp	3	-141.4	288.9	4.42	0.04	0.85
	Fn	3	-141.5	289.1	4.64	0.03	0.88
	AP	3	-141.6	289.1	4.66	0.03	0.92
	OV + Fp	4	-140.9	289.7	5.27	0.02	0.94
	OV + Fp + Fn + AP	8	-136.9	289.9	5.40	0.02	0.96
Pig / Cass	Fn (0.21)	3	-42.7	91.5	0.00	0.14	0.14

OV + Fp + AP	5	-40.7	91.5	0.06	0.14	0.28
DH + Fp + AP	3	-42.9	91.8	0.37	0.12	0.39
OV + AP	4	-41.9	91.8	0.37	0.12	0.51
OV + Fp + Fn + AP	8	-40.2	92.5	1.08	0.08	0.59
Fp	3	-43.3	92.7	1.19	0.08	0.67
DH + Fp + AP	7	-39.5	93.1	1.67	0.06	0.73
OV + Fp	4	-42.6	93.3	1.78	0.06	0.78
OV	3	-43.7	93.3	1.86	0.06	0.84
Random effects	2	-44.7	93.3	1.87	0.05	0.89
DH + AP	6	-40.8	93.6	2.18	0.05	0.94
DH + Fp + Fn + AP	8	-39.5	95.1	3.63	0.02	0.96

[a] K - Total number of model parameters including the intercept and residual variance

[b] Log($\mathcal{L}$) – Log likelihood

[c] Δi - Difference between model AICc and minimum AICc value

[d] Wi - Probability of model i being the best in this set of candidate models

The best models determined by AICc for predicting both presence and abundance of lagomorph faeces were those which included percentage of open vegetation (OV) (Tables 3.2, 3.3 and 3.4). At Cass, lagomorph faeces presence and abundance were best explained by the model which included OV, presence of fruiting species (Fp) and animal pathways (AP), however, the probability of support for this top model was low (Akaike weight (W_i) = 0.29) for faeces presence but high for faeces abundance (W_i = 0.90). A Δ_i of just 2 between the best model and the next four top models for hare faeces presence at Cass (i.e. all models with OV included) suggests these all have substantial support and suggest that any model including OV explains faeces presence reasonably well (Table 3.2, 3.4). The other variables present in these models (Fp and AP) are likely to be pretending variables. (A pretending variable is not biologically important but nonetheless appears within a "good" model due to the way AICc is calculated (see Anderson, 2008, pp. 65)). For lagomorph faeces abundance at Cass, however, the model including OV, Fp, Fn and AP was clearly the best (Δ_i of nearly 5). At Temple Basin, the single predictor model with OV was the best model explaining presence and abundance of lagomorph faeces. Overall, habitat with a higher proportion of open vegetation had a higher mean number of hare and rabbit faeces than shrubby and forested areas at both Cass and Temple Basin (Figure 3.3).

Models which included dominant habitat (DH) as a predictor of possum faeces presence and abundance were the best in the set of candidate models. Mean possum faecal densities were higher in forest habitat than in open or shrubby habitat (Figure 3.3).

The presence of sheep faeces was best explained by the null model (transect and subsite (random) effects) rather than any particular habitat variables or whether fruits were present.

However, the abundance of sheep faeces was best explained by models which included OV and AP. The best model (OV + AT) had a high probability of support (W_i = 0.58). The top models predicting sheep faeces presence vs. faeces abundance were vastly different, suggesting that sheep visit and defaecate in some transects more than others, but large quantities are found in areas determined by OV and AP. Where sheep faeces were present, mean densities were higher in plots with a larger proportion of open vegetation (Figure 3.3).

Table 3.3 Summary results for the selected top models used to explain the **abundance** of faeces for each animal type at both sites: Cass and Temple Basin (where n was large enough to allow analysis). A set of 14 *a priori* (linear mixed effects) models was formulated and the best models were selected based upon the Akaike Information Criteria (AICc), with the top models having a cumulative Akaike weight (Cum. wi) ≥ 0.95 to make up a 95% confidence set. Model terms presented below show all fixed effects predictors only (but random effects transect/site are included in all models). Adjusted R^2 are presented for the best model only. Abbreviations for the predictors are: OV = proportion of open vegetation; DH = dominant habitat; AP = animal pathways; Fp = presence of fruiting species; Fn = number of fruiting species.

Species / Site	Model	K[a]	log(ℒ)[b]	AICc	Δ*i* [c]	W*i* [d]	Cum.w*i*
Lagomorph / Cass	OV + Fp + Fn + AP (0.22)	6	-1623.5	3259.1	0.00	0.90	0.90
	OV + Fp + AP	5	-1626.9	3264.0	4.90	0.08	0.98
Lagomorph / Temple	OV (0.07)	3	-2652.3	5310.6	0.00	0.44	0.44
	OV + AP	4	-2651.8	5311.7	1.17	0.24	0.68
	OV + Fp	4	-2652.2	5312.4	1.84	0.17	0.85
	OV + Fp + AP	5	-2651.8	5313.6	3.03	0.10	0.95
Possum / Cass	DH + AP (0.27)	6	-898.9	1810.0	0.00	0.21	0.21
	DH + Fp + Fn + AP	8	-896.8	1810.1	0.05	0.20	0.41
	DH	5	-900.0	1810.1	0.14	0.20	0.61
	DH + Fp + AP	7	-898.7	1811.8	1.80	0.09	0.70
	DH + Fp	6	-899.8	1811.8	1.80	0.09	0.78
	OV + Fp + Fn + AP	6	-899.8	1811.8	1.83	0.08	0.86
	OV + AP	4	-902.2	1812.6	2.60	0.06	0.92
	OV	3	-904.0	1814.1	4.11	0.03	0.95
Sheep / Cass	OV + AP (0.43)	4	-4293.7	8595.5	0.00	0.58	0.58
	OV + Fp + AP	5	-4293.3	8596.9	1.40	0.29	0.88
	OV + Fp + Fn + AP	6	-4293.1	8598.6	3.09	0.12	1.00

[a] K - Total number of model parameters including the intercept and residual variance

[b] Log(ℒ) – Log likelihood

[c] Δ*i* - Difference between model AICc and minimum AICc value

[d] W*i* - Probability of model *i* being the best in this set of candidate models

Hedgehog and pig faeces numbers were low and model sets for both animals had low levels of certainty, with nearly all of the 14 candidate models included in the 95% confidence set (Table 3.2). However, dominant habitat was a weak predictor of hedgehog faecal abundance, featuring in the top three models, with greater numbers found in open vegetation compared with forest and shrubby habitat.

Table 3.4 Summary of the most important predictors for the presence (Δ) and abundance (√) of faeces for each animal type. Predictors were chosen from top models only (with Δ*i* of ≤ 2). All data are from Cass except where specified otherwise. * All models for pig faecal presence were poorly fitting (adjusted R^2 value = 0.2) and had low Akaike weights, (i.e., no predictors adequately explained variation in the presence of pig faeces).

	Dominant Habitat	Open vegetation	Animal Pathways	Presence of fruiting species	Number of fruiting species	Null model
Sheep		√	√	√		Δ
Possum	Δ √		Δ √	Δ √	√	
Lagomorph		Δ √	Δ √	Δ √	√	
Lagomorph (TB)		Δ √	Δ √	Δ √		
Hedgehog	Δ		Δ	Δ		
Pig*						

Video Monitoring

Of the 425 hours of video camera surveillance, 15 discrete events (when an animal came into view and performed any activity) occurred. Of these events, seven were confirmed as fruit-feeding activity while the others were invertebrates (weta and spiders) and skinks (*Oligosoma* sp.) moving around but not feeding on fruit. The cameras captured a pipit (*Anthus novaeseelandiae*) eating fruits of *L. colensoi*, an unidentified bird (probably exotic finch *Fringilla* sp.) eating *G. depressa* fruit, possums handling and eating *G. depressa* fruit, skinks eating *C. propinqua* fruit, hedgehogs eating fruits of *L. colensoi* and *C. petriei*, and a ship rat (*Rattus rattus*) eating *L. colensoi* fruit. The video footage of the rat eating fruit provides evidence for a species that was not detected at all from faecal monitoring transects.

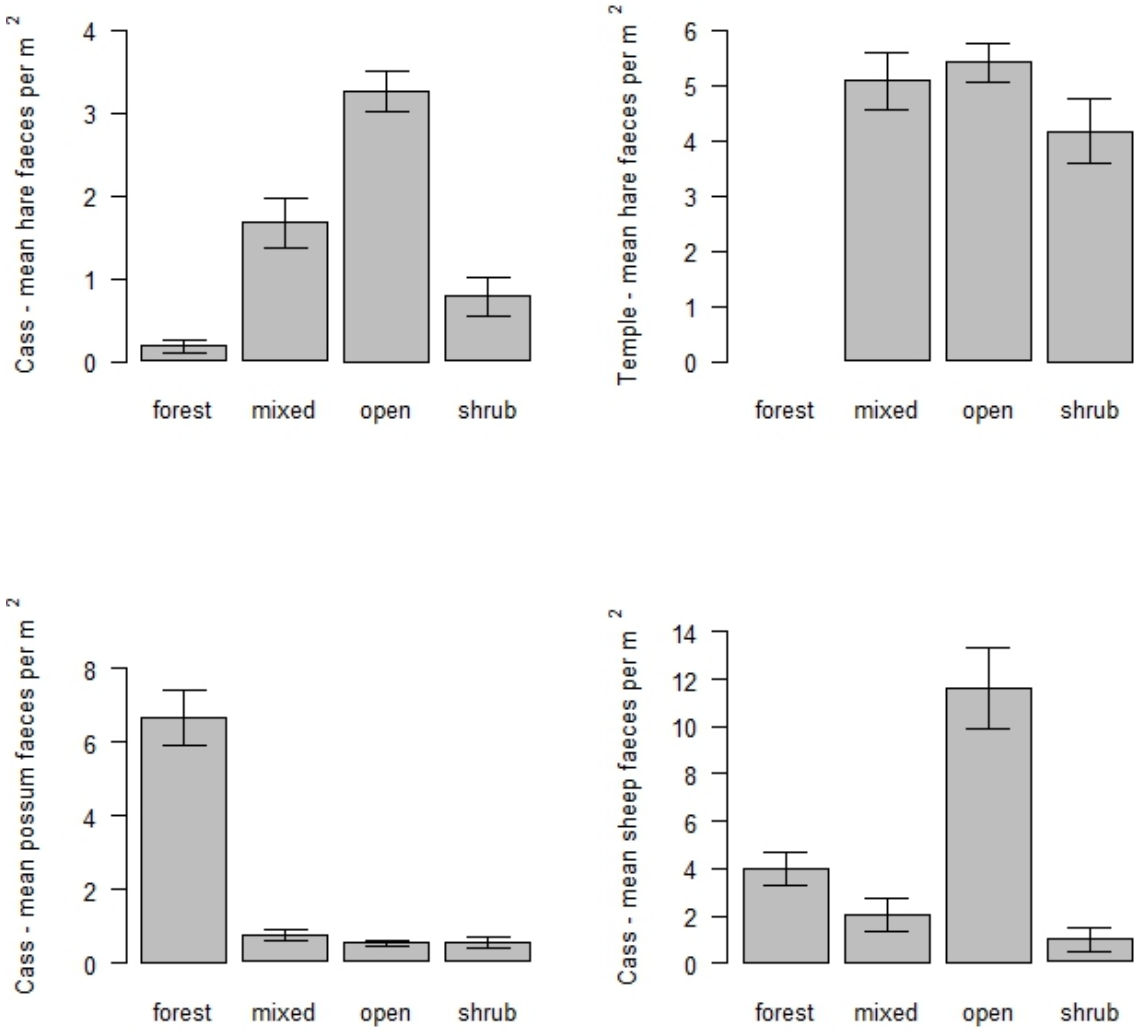


Figure 3.3 Mean (± 1 se) number of faeces for hares, possums and sheep by habitat type at Cass and hares at Temple Basin (top right). Data are not presented for other animal species due to low counts. Means shown here include all data (including 0 counts).

Discussion

Introduced mammals make a major numerical contribution to seed dispersal of New Zealand alpine plants, both in terms of the large quantities of fruit eaten and the number of seeds that are defaecated intact. Introduced mammals collectively dispersed seeds of more than 65 plant species at a rate of nearly 300 seeds m^{-2} yr^{-1}. Although globally there are numerous community-

level analyses of dispersal networks, most use frugivore visitation observation data, and are made up of co-evolved systems. In contrast, the dispersal network in this study system is mostly comprised of novel species interactions (incorporating exotic species introduced since human arrival in New Zealand) and incorporates dispersal quality aspects. One limitation of this study, however, was difficulty of detection of smaller faeces, such as those from birds, lizards and invertebrates – effectively the entire native disperser fauna – thus making it difficult to directly compare the relative contribution by native and introduced faunas. The numbers of faeces in Table 3.1 is probably accurate for mammals, while under-representing bird and lizard faeces. I opportunistically collected 38 lizard faeces from Cass using artificial retreats (Lettink et al., 2008) (not on transects); of these, only six contained a single whole seed (all *Coprosma petriei*) and one contained unidentified seed fragments. Most lizard faeces were dominated by invertebrate remains, suggesting that fruit is only eaten occasionally (see also Lawrence, 1997). A separate study by Young et al. (2012) (see Chapter 4) which combined detailed avian frugivore observations and faecal analyses, showed that birds were important seed dispersers for many alpine plants. In particular, the alpine kea parrot (*Nestor notabilis*) was the most important native avian seed disperser for alpine fruits, consuming more fruit and excreting most seeds intact compared with all other birds combined. Kea are also likely to make more significant contributions to regular long-distance dispersal events, especially between mountain ranges, compared with even the largest mammals.

The effectiveness of introduced mammals as seed dispersers

There has been a recent call in the literature for more information about whether introduced mammals are important for seed dispersal in New Zealand, especially for large mammals (pigs, goats, deer and sheep) (Kelly et al., 2010). Most of the relevant New Zealand literature in this area concerns forest plants with large seeds, lowland seral vegetation or weedy species. Here I assess the contribution by the various mammalian dispersers for seed dispersal effectiveness in New Zealand's alpine flora.

Possums

There has already been debate about whether possums are important for native seed dispersal in New Zealand (Dungan et al., 2002) or not (Williams et al., 2000, 2003). Fruit is known to be an important component of possum diet (Nugent et al., 2000) and is often preferred over foliage (Williams, 1982; Coleman et al., 1985; Cowan, 1990; Parkes and Thomson, 1995;

Nugent et al., 2001). During the 16 month period of this study, possums contributed around 78% to the dispersed seed rain. Almost all seeds (96%) were voided intact, although studies with lowland plants have reported lower values (Williams et al., 2000 and Dungan et al., 2002). Dungan et al. (2002) found that 75% of *Muehlenbeckia australis* seeds from possum faeces were visibly damaged and none of these intact defaecated seeds germinated (compared with 40% germination in control seeds). Seeds of most native alpine plants are tiny and many others have hard seed coats, which many aid in surviving gut passage intact. I found that for *Muehlenbeckia axillaris*, seeds commonly germinated within several weeks, even when sitting inside a petri dish with remnants of faecal matter. Even *M. axillaris* seeds with visible cracking germinated. However, long-term field germination experiments (see Chapter 5) have shown that germination in some other alpine species is normally very slow; the first *Leucopogon fraseri* and *L. colensoi* seeds have only just begun to germinate after 3 years, suggesting it takes a long time for the seed coat to naturally break down in field conditions.

Mean gut retention times are 1.5-3 days for possums (Nugent et al., 2000) and home range sizes are commonly 1-10 ha (Williams et al., 2000). Consequently, possums have the potential to move seeds considerable distances within a foraging area. However, if there is adequate food supply within a good feeding area there may be little incentive for long distance movement. Possums can detrimentally impact recruitment in forests through seedling herbivory (Wilson et al., 2003), and it is likely they may also have similar impacts above the treeline.

Hedgehogs

Hedgehogs were more frugivorous and more active in the New Zealand mountains than commonly thought (Jones and Sanders, 2005). I found hedgehog faeces up to 1400 m a.s.l. at both study sites, and during peak fruiting season many hedgehog faecal samples were dominated by seeds, fruit skins and leaf fragments. Some samples consisted of plant material only, with no invertebrate traces at all. This suggests that fruit may form a seasonally important component of hedgehog diet in dryland high-country habitat. Seeds of the divaricate shrub *Coprosma propinqua* were numerous in faecal samples found at these sites outside the study transects (therefore not presented in these results). It is not known whether hedgehogs were climbing *C. propinqua* shrubs to eat fruits, or concentrating on fallen fruits on the ground. I also found skink (*Oligosoma* sp.) remains in two hedgehog faecal samples, plus other samples that included large native invertebrates such as weta and carabid beetles, so hedgehog predatory impacts on small native

animals which are occasional seed dispersers (Larson and Burns, 2012; Young et al., 2012)) should be considered.

Areas covered by hedgehogs vary considerably from 0.5 to 50 ha, but within its home range an individual will typically move within a central core area of between 1.4 and 8 ha (Jones and Sanders, 2005). Video analysis and evidence of faecal samples along animal pathways suggests that hedgehogs heavily utilise these tracks, perhaps limiting potential seed deposition sites. I had insufficient data to analyse hedgehog faeces in relation to habitat, but most seeds were dispersed intact and into open grassland or mixed scrub which are habitat suitable for germination (see Chapter 5). However, dispersal events by hedgehogs are probably confined to within a single mountain or mountain range.

Lagomorphs

Lagomorphs are not generally known to be frugivorous in New Zealand (King, 2005), however, my results show that both hares and rabbits can include large quantities of fruit in their diets. Lagomorphs were responsible for nearly 13% of the dispersed seed rain in this study, dispersing intact seeds of 18 different plants. *Leucopogon colensoi* and *G. depressa* were the seeds most commonly found in lagomorph pellets. Although lagomorphs can maximise the digestion of cellulose by the process of coprophagy, surprisingly seeds emerged mostly intact. This could be due to the tiny seed sizes (e.g., *G. depressa*) and the durability of the seed coat (e.g., *Leucopogon* spp.).

Movements by hares are usually from near forest edges during the day where they rest, to feed on alpine plants at night. Hares may travel 1-2 km per night to feed (but may move 15 km in a night while feeding in the alpine zone) (Norbury and Flux, 2005). The home range size of rabbits is usually 2.5-2.8 ha (Norbury and Reddiex, 2005). Hares use pathways regularly for travel through tall grassland. Although much of the literature suggests that lagomorphs use preferred latrine sites (Norbury and Flux, 2005 and references therein), I found that lagomorph pellets were distributed widely and sparsely rather than clumped. Faecal densities were highest in areas dominated by open grassland vegetation with mixed scrub. Both hares and rabbits were found up to 1700 m a.s.l (Temple Basin) and are capable of high quantity and quality seed dispersal of alpine plants, but probably largely within a mountain range.

Large ungulates (sheep, pigs, deer and chamois)

Sheep contributed to about 2.5% of dispersed seed rain of more than 25 plant species. Many of these were unidentified seed specimens, possibly of grass and small herbs, often occurring as one-off or infrequent dispersal events. This suggests that those seeds were probably ingested unintentionally while grazing on foliage. Thus, sheep moved relatively low quantities of seeds relative to the many faeces produced. Since sheep are domestic stock, long-distance movement of seeds is probably affected mainly by farm management decisions.

I found few faeces deposited by large, wide-ranging ungulates such as red deer and chamois during this study, reflecting the low densities of these mammals at the sites. Given the low numbers of seed in faecal deposits of these animals, it is likely that ingestion of fruit was a by-catch during foliar browsing or grazing. Deer and chamois pellets are usually found in large clumps at latrine areas (Forsyth, 2005; Nugent and Fraser, 2005), concentrating dispersal of seeds into particular sites. More data are still needed to determine the role of these large grazing ungulates, especially in long distance seed dispersal events. However, given that most seeds are dispersed intact, albeit at low densities, and that home range sizes of wild red deer and chamois can be large (100-2074 ha and 138-656 ha respectively), occasional long distance dispersal events for some small-seeded alpine plant species are likely. In their native ranges of Europe, red deer are important seed dispersal agents for many plant species and contribute towards regular long-distance dispersal events (Welch, 1985; Malo and Suárez, 1995; Oheimb et al., 2005).

Although my study areas were outside the range of Himalayan tahr (*Hemitragus jemlahicus*), some alpine areas in the central Southern Alps hold large numbers and their potential for seed dispersal events should be investigated. Tahr commonly browse subalpine fleshy-fruited plants such as *P. nivalis*, *Gaultheria* and *Coprosma* spp. (Forsyth and Tustin, 2005), thus the probability of ingesting fruits and dispersing seeds is high.

Pigs appeared to select large numbers of fruits from certain species (e.g., *Rubus cissoidies* and *C. propinqua*), and surprisingly high numbers of seed were intact following gut-passage. O'Connor and Kelly (2012) assessed the role of pigs in seed dispersal for a large-seeded forest tree (matai, *Prumnopitys taxifolia*) and found that defaecated seeds germinated well compared with hand-cleaned seeds. Gut passage times are long (3-5 days) but most feral pigs are relatively sedentary and move from 0.2 to 2 km per day (McIlroy, 2005). Movements are related to abundance of food in an area and pigs probably range within good feeding grounds for concentrated periods of time before moving to new patches. Based on this, long distance movement of seeds is probably only intermittent. Any benefits of pigs as seed dispersers is counterbalanced by the destruction they cause by rooting the ground over and facilitating the

invasion of weeds such as *Hieracium* spp. Pigs also disperse seeds of weeds such as banana passionfruit (*Passiflora mollisima*) (Beavon, 2007).

The importance of assessing qualitative components of seed dispersal networks

Seed dispersal by frugivores contributes to the spatial patterns of plant populations (Cousens et al., 2008). By determining the effectiveness of distinct dispersal agents, studies should ideally link disperser behaviour with spatially explicit patterns of seed arrival (Schupp et al., 2010). Frugivores can display plant-specific variation in handling behaviour, quantity of seed removed, effects of gut passage on seed germination, patterns of movement, and dispersal distance. These factors may influence both seed viability and the spatial patterns of seed deposition (Howe, 1989; Wenny and Levey, 1998; Westcott et al., 2005; Muller-Landau et al., 2008). Many studies have shown how dispersed seeds can experience different mortality rates when dispersed across a variety of habitats and microsites (Schupp and Fuentes, 1995; Levine, 2000). In New Zealand, however, studies quantifying disperser effectiveness incorporating both quantitative and qualitative aspects are rare (with the exception of Williams et al., 2000; Dungan et al., 2002; Wotton 2002).

Analysing both the quantitative and qualitative aspects of seed dispersal (as outlined above) is vital to understand the overall contribution of each disperser. It was possible to understand how effectiveness changed among the various phases of the dispersal service, from quantity and diversity of species dispersed, to seed treatment in the gut and suitability of deposition site. My results show that, overall, any detrimental effects of gut passage on visible seed condition appeared to be minimal. Most mammals dispersed more than 95% of defaecated seeds intact, with the exception of deer where 90% were intact. However, when seed deposition site is also considered, seed dispersal effectiveness by introduced mammals decreases. Some mammals that dispersed large numbers of seeds (e.g., possums) generally defaecated in microsites less suitable for seed germination, growth and survival of several fleshy-fruited plant species (see Chapter 5). For example, possums moved the majority of seeds from grassland/shrubland, where the fleshy fruited species occur, into beech (*Nothofagus*) forests. Only a few alpine fleshy-fruited plants (e.g., *Podocarpus nivalis* and *Gaultheria* spp.) can germinate and survive in forests, but even these were largely restricted to edges at the study site.

A species that appears to have little quantitative participation in a dispersal network could be one of the most important dispersers if other aspects of dispersal, such as gentle gut treatment and good deposition site, are also considered. Conversely, species that appear to be important in a

frugivory network graph may prove less important when additional aspects of frugivore behaviour and habitat heterogeneities are considered (Carlo and Yang, 2011). If important underlying spatial, temporal and behavioural heterogeneities are not considered, a network may be unable to identify the agents important for seed dispersal and thus fail to correctly assess community organisation and dynamics. For example, Carlo and Yang (2011) re-assessed a previously published frugivory network (Carlo et al., 2003) which did not originally model processes of seed arrival to pasture habitat from surrounding forest in Puerto Rico. They assessed the importance of each frugivorous bird species for the stability of a forest community (defined as the ability of a forest community to regenerate after deforestation). They originally hypothesised that the most generalist species (nodes which interact with the greatest number of species, and have the greatest interaction frequency) would be the most important agents of seed dispersal into pastures. They identified the top three frugivore generalists in the network (Carlo et al., 2003) but found that the ninth ranked species (*Tyrannus dominicensus*) was actually the most active bird in pastures where they fed on insects, crossing from forests where they fed on fruits, and hence contributed most to the stability of the forests in Puerto Rico. Thus, the insect-dominated diet of *Tyrannus* disguised its importance as the key disperser in the frugivory network. The three most generalist species in their study also lacked significant activity in pastures and thus played little or no role in the early stages of forest succession from pasture.

My results show a similar pattern, where at first glance it would appear as though introduced mammals, particularly possums, are usefully dispersing many native seeds for a flora now devoid of many of its original dispersers. But upon closer inspection, possums are largely a black hole for seeds by eating large quantities of fruit and depositing the seeds into locations which are largely unsuitable for alpine plant establishment.

Introduced mammals as replacement dispersers: how do they compare with native fauna?

Can introduced mammals replace native birds as seed dispersers for the alpine flora? How do mammals compare in importance with native frugivores? Since many areas worldwide are facing fast-paced defaunation (Peres and Palacios, 2007) it is imperative to first understand the implications of past extinctions on the population structure of the living plants in order to predict the effects of ongoing extinction of the seed dispersers (Guimares Jr et al., 2008). The loss of large-bodied frugivores, capable of transporting large numbers of large seeds over long distances, has caused increased population differentiation because of a dramatic loss of potential for gene flow via seed (Jordano et al., 2007). However, in New Zealand, very little is known about the

historic disperser fauna and their role in shaping plant communities (Atkinson and Millener, 1991; Thorsen et al., 2011), therefore making it difficult to understand the impacts of their extinctions on the flora. If potential replacement seed dispersers such as introduced mammals in the New Zealand alpine system are in both direct and indirect competition with the native dispersers (birds, lizards and invertebrates), management efforts should still focus on conservation and protection of native species to perform functional roles in ecosystems (such as seed dispersal). It would be unwise to rely on the novel dispersal agents to perform such roles while we can still focus our efforts on retaining the high quality co-evolved dispersal by native birds such as kea, because introduced species both compete for resources and directly predate on birds. In certain areas of New Zealand, where most of the alpine fauna has now been eliminated, the flora may be largely reliant on exotic mammalian frugivores to disperse seeds, but the net benefits should be weighed against their negative direct and indirect impacts. Introduced small mammals may also affect regeneration by either dispersing or destroying the seeds of fleshy-fruited species during the chewing or handling process (Williams et al., 2000), or by grazing the seedlings (Burrows, 1994; Wilson et al., 2003), while large grazing mammals can disrupt the process completely (Wilson, 1994). Indirect impacts of introduced mammals also include selective browsing causing near-extinctions of certain plant species, rooting, trampling and prevention of potential re-establishment of populations of native fauna into such areas through competition and predation.

Using faecal sampling methods to assess seed deposition into various microhabitats is advantageous and in general provides a simple method that should be utilised more in studies assessing seed dispersal effectiveness by a given animal. It should be noted that mammal faecal abundance in the study areas indicates their relative abundance and activity in these areas. The relative contribution of each species as a seed disperser is therefore likely to change as their abundance changes. Densities of mammals at Temple Basin are probably lower than many other alpine areas around the Southern Alps because of its frequent use for recreational activities such as climbing and skiing. Therefore, the potential for seed dispersal by introduced mammals in other National Park areas could be higher.

Conclusions

Frugivores can differ drastically in their ability to link isolated or naturally fragmented patches (Jordano et al., 2007) such as mountain tops. Frugivores therefore may differ in their quality of deposition, thus investigating the effect of dispersal distance can critically alter conclusions about disperser effectiveness (Spiegel and Nathan, 2007). Native frugivores (kea) are

probably responsible for the most regular long distance dispersal events (daily). Large ungulates such as pigs, deer and chamois are likely to contribute to occasional long-distance dispersal events (dependent on how long they focus on a particular foraging area and feed above treeline), while small mammals and native birds, lizards and invertebrates most likely to disperse seeds within a mountain or range. By incorporating dispersal distance and seed deposition sites into the disperser effectiveness framework, this study has begun to provide a more comprehensive understanding of the relative effectiveness of introduced mammals towards ecosystem functions such as seed dispersal.

APPENDIX 3.1 Species list and codes for dispersed species

Table A3.1. Species level identification codes and names (to the highest taxonomic level possible) for each seed type (n = 67) found in faecal samples to enable interpretation of the community dispersal bipartite network (see Fig. 3). Species are ranked according to disperser richness. Most of the top 20 seed types have multiple dispersers and are fleshy-fruited. Unidentified species (labelled with "u") mostly consisted of just a few samples, making identification difficult. Codes for animal dispersers (n = 10) are as follows: B = Bird; C = Chamois; D = Deer; G = Grasshopper; L = Lagomorph; H = Hedgehog; K = Kea; PI = Pig; P = Possum; S = Sheep.

Seed ID code	Taxonomic name	Family	Fleshy-fruited	Number of dispersers	Animal Dispersers
GD	*Gaultheria depressa*	Ericaceae	yes	9	B,C,G,L,H,K,PI,P,S
LC	*Leucopogon colensoi*	Ericaceae	yes	8	B,C,L,H,K,PI,P,S
CS	*Coriaria sarmentosa*	Coriariaceae	yes	7	D,L,H,K,PI,P,S
LF	*Leucopogon fraseri*	Ericaceae	yes	6	B,L,H,K,P,S
MA	*Muehlenbeckia axillaris*	Polygonaceae	yes	6	B,L,K,PI,P,S
MN	*Myrsine nummularia*	Myrsinaceae	yes	5	B,L,PI,P,S
CSE	*Coprosma serrulata*	Rubiaceae	yes	5	B,L,H,P,S
CA	*Colobanthus acicularis*	Caryophyllaceae		4	C,L,P,S
CC	*Corokia cotoneaster*	Escalloniaceae	yes	4	B,L,P,S
PN	*Podocarpus nivalis*	Podocarpaceae	yes	4	L,H,K,P,S
CPE	*Coprosma petriei*	Rubiaceae	yes	4	B,L,H,P
CPR	*Coprosma propinqua*	Rubiaceae	yes	4	B,L,PI,P
CPL	*Coriaria plumosa*	Coriariaceae	yes	3	L,P,S
cyp1	*Cyperaceae* 1	Cyperaceae		3	PI,P,S
CJ	*Cyathodes juniperinum*	Ericaceae	yes	3	B,K,P
Jun	*Juncus* sp	Juncaceae		3	L,P,S
RC	*Rubus cissoides*	Roseaceae	yes	3	L,PI,P
CCH	*Coprosma cheesemannii*	Rubiaceae	yes	3	K,P,S
u19				3	B,L
HH	*Hydrocotyle hydrophila*	Araliaceae	yes	2	P,S
AF	*Aristotelia fruticosa*	Elaeocarpaceae	yes	2	K,PI
PD	*Pittosporum divaricatum*	Pittosporaceae	yes	2	P,S
PC	*Phormium cookianum*	Xanthorrhoeaceae		2	P,S
u10				2	P,S
u22				2	L,P
u24				2	P,S
Hyd	*Hydrocotyle* sp	Araliaceae	yes	1	L
RSI	*Raukaua simplex*	Araliaceae	yes	1	S
Myo	*Myosotis* sp	Boraginaceae		1	S
cyp2	*Cyperaceae* 2	Cyperaceae		1	S
IF	*Isolepis fluitans*	Cyperaceae		1	S
LG	*Liparophyllum gunnii*	Menythaceae		1	S
LS	*Leptospermum scoparium*	Myrtaceae		1	P
NS	*Nothofagus solandri*	Nothofagaceae		1	P
DT	*Discaria toumatou*	Rhamnaceae		1	P

RA	*Rubus australis*	Roseaceae	yes	1	H
RR	*Rosa rubiginosa*	Roseaceae	yes	1	P
RS	*Rubus schmidelioides*	Roseaceae	yes	1	P
CD	*Coprosma depressa*	Rubiaceae	yes	1	L
Gal	*Galium* sp	Rubiaceae		1	L
PS	*Pimelea sericiovillosa*	Thymeliaceae	yes	1	S
u1				1	S
u2				1	P
u3				1	P
u4				1	L
u5				1	S
u6				1	P
u7				1	P
u8				1	P
u9				1	P
u11				1	P
u12				1	P
u13				1	S
u14				1	P
u15				1	P
u16				1	S
u17				1	S
u18				1	L
u20				1	B
u21				1	P
u23				1	H
u25				1	S

APPENDIX 3.2 Percentages of seeds dispersed intact versus fragmented

Table A3.2 Seed condition after gut passage through the different animal dispersers

	Seed condition after gut-passage	
Species	% dispersed intact	% fragmented
Deer	90.0	10.0
Birds	91.6	8.4
Kea	95.7	4.3
Hare	96.2	3.8
Possum	96.6	3.4
Pig	97.4	2.6
Sheep	98.0	2.0
Hedgehog	98.5	1.5
Chamois	99.3	0.7
Grasshopper	100.0	0.0

APPENDIX 3.3 List of all candidate models used for presence and abundance data

List of all candidate models for used for presence dataset

1. Faeces present ~ *DH* + *Fp* + *Fn* + *AP*, family = binomial # Full model (all terms)
2. Faeces present ~ *OV* + *Fp* + *Fn* + *AP*, family = binomial # Full model (all terms)
3. Faeces present ~ *DH* + *Fp* + *AP*, family = binomial
4. Faeces present ~ *OV* + *Fp* + *AP*, family = binomial
5. Faeces present ~ *DH* + *Fp*, family = binomial
6. Faeces present ~ *OV* + *Fp*, family = binomial
7. Faeces present ~ *DH* + *AP*, family = binomial
8. Faeces present ~ *OV* + *AP*, family = binomial
9. Faeces present ~ *DH*, family = binomial
10. Faeces present ~ *OV*, family = binomial
11. Faeces present ~ *Fp*, family = binomial
12. Faeces present ~ *Fn*, family = binomial
13. Faeces present ~ *AP*, family = binomial
14. Faeces present ~ 1 # NULL model (Random effects only)

List of all candidate models for used for abundance dataset

1. Faeces per m^2 $year^{-1}$ ~ *DH* + *Fp* + *Fn* + *AP*, family = poisson # Full model (all terms)
2. Faeces per m^2 $year^{-1}$ ~ *OV* + *Fp* + *Fn* + *AP*, family = poisson # Full model (all terms)
3. Faeces per m^2 $year^{-1}$ ~ *DH* + *Fp* + *AP*, family = poisson
4. Faeces per m^2 $year^{-1}$ ~ *OV* + *Fp* + *AP*, family = poisson
5. Faeces per m^2 $year^{-1}$ ~ *DH* + *Fp*, family = poisson
6. Faeces per m^2 $year^{-1}$ ~ *OV* + *Fp*, family = poisson
7. Faeces per m^2 $year^{-1}$ ~ *DH* + *AP*, family = poisson
8. Faeces per m^2 $year^{-1}$ ~ *OV* + *AP*, family = poisson
9. Faeces per m^2 $year^{-1}$ ~ *DH*, family = poisson
10. Faeces per m^2 $year^{-1}$ ~ *OV*, family = poisson
11. Faeces per m^2 $year^{-1}$ ~ *Fp*, family = poisson
12. Faeces per m^2 $year^{-1}$ ~ *Fn*, family = poisson
13. Faeces per m^2 $year^{-1}$ ~ *AP*, family = poisson
14. Faeces per m^2 $year^{-1}$ ~ 1 # NULL model (Random effects only)

APPENDIX 3.4 Estimates and standard errors for top presence and abundance models

Table A3.4a Estimates and standard errors (in parentheses) for predictors featuring in only the top model in each set of candidate models for faecal presence data for each animal (TB = Temple Basin, all others are Cass). DH (f = forest), DH (s = shrub), DH (m = mixed), DH (o = open). Hare refers to hares and rabbits combined.

Animal	Intercept	DH(f)	DH (s)	DH (m)	DH (o)	OV	AT (y)	Fp (y)	Fn
Lagomorph	-0.36								
(TB)	(0.36)	-	-	-	-	0.01 (0.003)	-	-	-
	-2.54						0.35	0.26	
Lagomorph	(0.36)	-	-	-	-	-2.54 (0.36)	(0.19)	(0.16)	-
	0.35		-3.63	-2.96	-3.06			0.36	
Possum	(0.65)		(0.75)	(0.74)	(0.72)	-	-	(0.20)	-
	-3.53								
Sheep	(0.45)	-	-	-	-	-	-	-	-
	-5.07		-0.9	1.42	0.75				
Hedgehog	(0.87)		(1.39)	(0.96)	(0.93)	-	-	-	-
	-14.54								2.0
Pig	(6.6)	-	-	-	-	-	-	-	(1.05)

Table A3.4b Estimates and standard errors (in parentheses) for predictors featuring in only the top model in each set of candidate models for faecal abundance data for each animal (TB = Temple Basin, all others are Cass). DH (f = forest), DH (s = shrub), DH (m = mixed), DH (o = open). Hare refers to hares and rabbits combined.

	Intercept	DH (f)	DH (s)	DH (m)	DH (o)	OV	AT (Y)	Fp (Y)	Fn
	1.71					0.004			
Hare (TB)	(0.12)	-	-	-	-	(0.0005)	-	-	-
	1.12					0.01	-0.19	0.20	-0.25
Hare	(0.14)	-	-	-	-	(0.001)	(0.05)	(0.12)	(0.10)
	2.10		-0.19	-0.55	-0.49		-0.13		
Possum	(0.25)		(0.09)	(0.29)	(0.28)	-	(0.09)	-	-
	2.03					0.01	-0.73		
Sheep	(0.28)	-	-	-	-	(0.12)	(0.12)	-	-

CHAPTER FOUR

Alpine flora may depend on declining frugivorous parrot for seed dispersal

Juvenile kea having a break from feeding on red fruits of *Pentachondra pumila* at Cass.

(Photo: L.M. Young)

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Abstract

Globally, bird numbers are declining, with potentially serious flow-on effects on ecosystem processes, such as seed dispersal mutualisms. However, management to maintain seed dispersal may be inappropriate if unexpected animals are the most important dispersers. Numbers of the world's only alpine parrot, the New Zealand kea (*Nestor notabilis*), have declined drastically over the last 120 years after an intense period of official persecution. Today <5000 kea remain in the wild. Previously it has been assumed that like other parrots, kea would destroy most of the seeds they eat, thereby contributing little to seed dispersal. The New Zealand alpine flora is rich in fleshy-fruited species yet has a limited disperser fauna. Consequently, we investigated the relevance of kea as a seed disperser in New Zealand's alpine ecosystems. Field-based foraging observations coupled with faecal analyses showed kea were by far the most important extant alpine avian frugivore. Kea selected more fruiting species (21 vs. 17 species), consumed more fruit, and dispersed more seeds (8137 vs. 795) than all other birds combined. Rates of seed predation by kea were extremely low, and evident in only 25% of species eaten. Kea are the only species that make frequent long-distance flights within and between mountain ranges. Hence, much of the effective long-distance dispersal of the alpine flora may be currently performed by kea. Conservation of kea is therefore important both for ensuring the survival of the species and for their role in seed-dispersal mutualisms for which there are few extant substitutes.

Introduction

Understanding the role of mutualists within natural communities is important for predicting how their decline might alter plant communities (Anderson et al., 2011; Christian, 2001), and for associated conservation and management purposes (Garcia et al., 2010; Trakhenbrot et al., 2005). In addition to the global decline in the number of bird species, the number of individuals is estimated to have declined 20-25% in the last five centuries (Gaston et al., 2003). Avian populations and dependent ecosystem services are therefore probably declining faster than predicted by species extinctions because of "functional extinction" (Sekercioglu et al., 2004). Seed dispersal is one of the most influential avian ecological services (Howe and Smallwood, 1982; Sekercioglu et al., 2004). Globally, dispersal failure may be an increasing problem for many plant species (Christian, 2001; Corlett, 1998; Traveset and Riera, 2005), yet the botanical implications of avian frugivore extinctions and declines are poorly understood (Cordeiro and Howe, 2001).

Few studies experimentally link bird declines with plant declines (but see Anderson et al., 2011; Wenny et al., 2011; Wotton and Kelly, 2011 for evidence supporting this). New Zealand offers an excellent opportunity to understand the ecological consequences of bird declines, with only the "wreckage of an avifauna" (Diamond, 1984) remaining in an island situation that, barring three bat species, evolved without terrestrial mammals. Plant-animal mutualisms in New Zealand have almost certainly undergone major changes since the arrival of humans and the subsequent extinction or decline of many bird and lizard species (Holdaway, 1989; Towns and Daugherty, 1994; Kelly et al., 2010). Almost half (41%) of the endemic avifauna has gone extinct (Innes et al., 2010), including a number of known frugivores (Holdaway et al., 2001). Weakened pollination mutualisms in forest communities have already been demonstrated as an example of flow-on effects of bird decline in New Zealand (Anderson et al., 2011), and there is also concern about dispersal failure affecting large-fruited trees (Wotton and Kelly, 2011). Before human arrival in 1280 AD (Wilmshurst et al., 2008), birds were the major seed dispersers (Lord, 2004), with minor local contributions by lizards (Whittaker, 1987; Wotton, 2002) and invertebrates such as weta (Orthoptera) (Duthie et al., 2006).

Alpine ecosystems can be considered as naturally fragmented landscapes; spatially segregated 'islands' separated by seas of lower elevational forest (Halloy and Mark, 2003), analogous to indigenous forest remnants in a matrix of agricultural land. Dispersal of seeds between alpine areas is thus important for facilitating genetic connectivity between fragmented patches, maintaining metapopulation persistence, and promoting long-term species survival. In New Zealand's alpine areas, which constitute around 13% of the total land area, little is known about animal-plant dispersal mutualisms. Fleshy-fruitedness is unusually common (12%) in the New Zealand indigenous alpine flora compared to other temperate alpine plant communities (e.g. fleshy fruited species represent 3–5% of the alpine flora in Victoria, Australia and 5.4% in Chile) (Lord, 1999 and references therein). However, despite the preponderance of fleshy-fruited alpine species, there are few extant frugivores to disperse the seeds.

The kea (*Nestor notabilis*) is the world's only alpine parrot and is potentially the only remaining significantly frugivorous bird that lives and feeds in New Zealand's alpine zone (Bull, 1965; Clarke, 1970). (Note: for Maori names like kea, the plural does not take an "s"). Kea eat the fruit of a range of alpine plant species (Clarke, 1970; Jackson, 1960; Brejaart, 1988). These large, long-lived birds can fly long distances (c. 20-30 km) within and between different mountain ranges (Clarke, 1970; Elliott and Kemp, 2004). Worldwide, parrots are primarily seed predators (see Boyes and Perrin, 2010 and references therein) and, while seed predation has

typically been assumed for kea (Clout and Hay, 1989; Willson et al., 1989; Lee et al., 1991; O'Donnell and Dilks, 1994), evidence on seed survival after kea ingestion is scarce.

Kea populations have undergone very large declines because of an intensive campaign of official persecution, justified by occasional kea attacks on farm animals (Marriner, 1908). This is one of the worst cases of avicide in New Zealand's recent history. From the late 1800's, the government placed a bounty on kea beaks. In the 1920's, the bounty was 10 shillings per beak, equating to $65 (NZD) today (Temple, 1996). This provided a clear incentive to kill birds even in protected areas (Pullar, 1996). Only in 1971, after an estimated 150,000 kea had been killed (Cunningham, 1948) did the bounty cease. In 1986 kea were finally given full protection, but some individuals are still destroyed if they are known to attack sheep. Currently, only an estimated 1000–5000 individuals remain in the wild (Anderson, 1986). Kea are listed as an 'at risk' species by the New Zealand Department of Conservation (DoC) (Miskelly et al., 2008) and 'vulnerable' by the IUCN (2010) and numbers continue to decline (DoC and Kea Conservation Trust, unpubl. data). In addition to illegal hunting and pet trade activities, other major threats to kea populations include predation, competition for resources with introduced mammals and humans, lead poisoning from anthropogenic causes, and habitat degradation (Pullar, 1996).

We tested to what extent kea ingest and defecate intact seeds from various plant species, and their relative importance for seed dispersal in the alpine zone. We quantified: (i) the relative numerical contribution to frugivory and seed dispersal by kea compared with other birds in the alpine zone, (ii) what plant species kea fed on, and how this compared to fruit availability, and (iii) whether kea provided a high quantity and quality of dispersal through the proportion of seeds ingested and dispersed intact.

Methods

Study species and sites

Kea measure 45–50 cm in length (mean weight: 780 and 960 g for females and males, respectively) and live in complex, stratified social systems (Diamond and Bond, 1999). They typically live between 700 m and 2000 m in altitude in the Southern Alps of New Zealand, a habitat composed predominantly of southern beech (*Nothofagus*) forest and alpine grasslands (Jackson, 1960). Kea feed on a range of food items, including invertebrates and fruit, leaves, roots and flowers of over 100 plant species (Brejaart, 1988). Kea tend to form larger flocks from January (Jackson, 1960; Clarke, 1970) and forage above the treeline during the summer period

before dispersing into smaller flocks in autumn and retreating to lower altitudes during winter (Jackson, 1960).

Our two study sites were about 180 km apart in the Southern Alps: Red Tarns, Mt Sebastapol, Mt Cook National Park (43°45’ S, 170°6’ E, 1000–1300 m a.s.l.) and Mt Sugarloaf, Cass, < 5 km east of the Arthurs Pass National Park eastern boundary (43°2’S, 171°4’E, 1000–1360 m a.s.l.). These sites were chosen because prior research established that these were important feeding areas for kea, which came from, and returned to multiple mountain ranges surrounding these mountains. There are no data on kea densities in these areas; however, both areas are known to be strongholds for kea. Feeding observations took place above the treeline in the subalpine zone consisting of scrub, shrubland, and grassland, with bare rock and scree habitat at both sites. At least 50 fleshy-fruited species within 24 genera and 14 families occurred at the sites (see Appendix 1, Table A1 for fruit trait details for most of these species). The fruit of some species ripens as early as December, with the peak fruiting season from January until May, although many fruits remain on plants over winter. We use the term “fruit” here in a functional sense to encompass seeds enclosed in or associated with a fleshy edible structure (e.g. drupes, berries or arils), i.e. species with seeds that are dispersed by passage through an animal’s gut. We use the term “alpine” to represent any habitat occurring above treeline (approximately 1100 m a.s.l).

Figure 4 Photograph taken from upper Red Tarns of Mt Sebastapol, Aoraki Mt Cook National Park, showing that these alpine habitats consist of low-growing, open vegetation making long-distance bird foraging observations easy.

Feeding observations

2009 fruiting season

To determine which bird species were present and feeding in alpine areas, we made foraging observations of birds other than kea ("non-kea feeding observations") during the 2009 fruiting season. Alpine habitats consist of low, open vegetation (Figure 4), making it easy to detect birds at large distances (often >300 m) and to observe them with binoculars without apparent effects on their behaviour. We slowly walked a similar route at Sugarloaf over ten non-consecutive days between January and April during the alpine fruiting season, before autumn snowfall. The route varied among days within a larger available foraging area on the mountain, guided by where fruiting species were located. Walks usually took 2–3 hours, covering ca. 3–5 km, stopping periodically to scan with binoculars, and were equally divided between the most active foraging periods in mornings (6–11 am) and evenings (4–9 pm) (Jackson, 1960) (although seldom within the same day). Every time we encountered a bird, we noted the food item eaten (plant, insect or other). We recorded the total number of observations for each bird species feeding on each food type (Galetti, 1993).

2010 fruiting season

We used the same methods as above to collect bird (non-kea) feeding observations between January and April 2010. Additionally, because the 2009 observations showed kea were important and very mobile dispersers, we incorporated kea-focused feeding observations when kea were encountered during these sessions (January to May 2010). Morning and evening kea-feeding observations were conducted for 10 days at each site and most sampling days fell non-consecutively. When kea were detected, we approached to within ten meters and observed them using binoculars. Kea feeding behaviour was not affected by our presence at these distances, possibly because of their historical lack of predators and neophilia (Diamond and Bond, 1999). The latter is a particularly useful characteristic of these birds that makes them amenable to study (e.g. Gajdon et al., 2004). Between one and three observers were present during each survey period, and usually spread out across the broad foraging area on the mountain to obtain independent samples. Some feeding data were recorded via direct observation while other data were captured using a high definition video (HDV) camera (Canon HV30, 10x optical zoom) to obtain more detailed feeding behaviour using zoom-in capabilities upon playback. We recorded 229 discrete feeding events (11 h in total), incorporating individuals from both sexes and all age

classes, although the majority of our observations were on juveniles and fledglings (see Appendix 1, Table A2). This preponderance of younger birds matches the age composition of typical kea flocks seen in the alpine areas, probably because young birds flock together to feed above the treeline while breeding adults most likely forage more locally in their territories (B. Barrett pers. comm).

For each feeding event we recorded: time of day (morning or evening), feeding duration (seconds), and food type (plant, insect or other). For plant material we recorded species, and part(s) eaten (fruit, aril, seed, flower, leaf, root, stem, whole or unknown). Finally, for fleshy-fruited species, we noted seed treatment method (ingested or rejected) where possible. One feeding event was classified as a discrete observation of a single bird feeding on a single food item for a certain length of time. If the bird left the plant to feed on a different item, it was recorded as a new event (Galetti, 1993). We tried to avoid sampling the same bird more than once in a session. To minimise pseudoreplication arising from potential group-influenced feeding behaviours, we avoided sampling mulitple birds from within a closely feeding group (especially multiple birds feeding on the same plant). We sampled only during non-rainy days, because we learned from the 2009 season that birds are much less active in the rain.

Food choice in relation to availability

We measured fruit abundance throughout the fruiting season to establish whether certain species were eaten by kea in proportion to their relative abundance and whether this changed over the fruiting season. We visually scored fruit abundance along thirteen 50 m line transects (six at Red Tarns, seven at Sugarloaf) within the general area where feeding observations were made. We sampled a circular plot using a string of 2 m radius (plot area = 12.56 m^2) every 10 m from 0–50 m. Plot centres were marked so the same area could be sampled at each re-measurement period. Within each plot (six per transect), we recorded the percentage vegetation cover of all fleshy-fruited species. For each fleshy-fruited species within the plots we then assigned a relative fruit abundance per unit area score (ranging from 0–10, with higher scores indicating higher levels of fruiting). We calculated cover-adjusted fruit abundance scores by multiplying the fruiting score by percent vegetation cover for each species in each plot. Mean fruiting scores were then calculated across plots for each site. To account for temporal variation in fruiting, we scored fruit abundance early, mid and late season and related this to kea fruit-feeding activity around each of those time periods. To have approximately equal numbers of field work days per time period, the data were divided into "early season" – all observations

before March 15 (Red Tarns = 57 kea feeding observations, Sugarloaf = 53 observations), "mid season"– March 15 to April 13 (Red Tarns = 78, Sugarloaf = 17 observations), and "late season" – April 14 to May 6, 2010 (no kea feeding observations).

To determine whether kea feeding changed significantly through the season, we used Generalised Linear Models (GLM's) with a gaussian error distribution for the four most-often eaten plant species to model the proportion of all feeding observations devoted to that species against the explanatory variables season (early or mid) and site (Red Tarns or Sugarloaf). We used the arcsine square root transformation to normalise the proportion of time spent feeding response variable. Three of the four plant species showed significant differences between early and mid season in the proportion of time kea spent feeding on the fruits (*P. nivalis* P = 0.003, *P. pumila* P = <0.001, *M. axillaris* P = 0.03, *G. depressa* P = 0.06, $df_{(1,202)}$). Site effects were also significant. We therefore kept data for each time period and site separate in the analysis of food choice in relation to availability. GLM's were done using the statistical package R version 2.13.1 (R Development Core Team, 2011).

Seed treatment

Preliminary observations indicated that when feeding on *Podocarpus nivalis*, kea sometimes use their beaks to separate the fleshy red aril from the seed, ingesting the aril and rejecting the seed directly back into or near the parent plant. Consequently, seed fates of *P. nivalis* were impossible to quantify using feeding observations alone. To determine whether rejected seeds were intact or destroyed during this type of feeding, we randomly collected 200 kea-processed *P. nivalis* seeds from the vicinity of three plants at Red Tarns and counted both the number of intact and damaged seeds.

Faecal sampling and gut-passage time

To determine the effects of gut passage on seed fate and to identify species eaten, we collected all fresh kea faeces (n = 65) and all other bird faeces (n = 35) found during this survey period. Faeces were searched for repeatedly across all microhabitat types (e.g. under shrubs, on scree slopes) to collect as many faecal samples as possible from all birds. Faeces were analyzed for seed species, recording seed numbers per faecal sample and visible condition of seeds (intact or fragmented), using a microscope (6–40 x magnification). Kea faeces are distinguishable from other birds because of the large size, distinctly darker colouring, and the absence of a white uric acid segment produced by most other birds present at these alpine sites. The characteristics of kea faeces were known from faeces produced by kea being handled for banding. Non-kea faeces

could not usually be distinguished between bird species; therefore all non-kea bird faeces were collectively referred to as coming from "other birds".

We tested gut passage times using six captive kea at Willowbank Wildlife Reserve, Christchurch, New Zealand. The birds were fed blueberries (*Vaccinium corymbosum*: Ericaceae) because their colour makes them easy to detect in faeces, and fruit have numerous tiny seeds similar to the confamilial *Gaultheria* spp. commonly eaten by wild kea. We recorded the length of time between when kea ate the berries and when they emerged in the faeces, finishing after 4.5 h, when seeds stopped coming through.

Statistical Analysis

We used Ivlev's electivity index (Ivlev, 1961) to calculate kea feeding selectivity ratios (SR). Ivlev's electivity index (E) is defined as: $E = (r-p)/(r+p)$ where r is the proportion of the food item in the diet and p is the proportion of food available in the environment. This provides an index ranging between -1 and +1, where values closer to -1 indicate an under-representation and values closer to 1 indicate an over-representation of the food item in the diet compared with the relative availability in the environment. To minimise effects of seasonal changes in fruit availability, selectivity calculations compared diet to availability within early, middle and late season as defined above. Following Forsyth et al. (2002), we used the following breaks for classification; $E > 0.3$, "preferred"; $-0.3 < E < 0.3$, "not selected"; $E < -0.3$, "avoided".

Results

Feeding observations

Twelve of the 20 observation days provided data on kea feeding (six at each site). On the other days, birds were either not present, present but not feeding, or feeding but too far away to positively identify foraging behaviour. We recorded a total of 229 discrete feeding observations on all food items (Red Tarns = 141, Sugarloaf = 88), totalling 652.37 minutes. At Red Tarns most feeding observations were in the mornings (94%), while at Sugarloaf most were in the evenings (82%). Feeding bouts ranged from 2–958 s and mean feeding bouts for morning and evening, respectively were: Red Tarns = 208 s and 206 s; Sugarloaf = 44 s and 166 s (see Appendix 1, Table A2).

We observed kea feeding on 13 different food items, including fruit from six fleshy-fruited plant species (Figure 4.1). Numbers of feeding observations were higher on fruit (n = 205) than on all other food items (n = 24). Moreover, kea spent considerably more time feeding on fruit than on

other foods. This was consistent between sites, with 93.7% of the observed feeding time dedicated to frugivory at Red Tarns and 83.5% at Sugarloaf. Five fruiting species were eaten by kea at Red Tarns, compared with only 3 species at Sugarloaf. All fruiting species eaten were present at both sites except for *Phyllocladus alpinus*, which was absent at Sugarloaf. Fruits of *P. nivalis* dominated kea diets at both sites, constituting over 60% of observed feeding time (Figure 4.1), and also comprising most of the feeding observations (Red Tarns n = 91, Sugarloaf n = 53). There were clear differences between sites in the proportion of time spent feeding on other species; e.g. kea fed on *Pentachondra pumila* for 18% of the time at Sugarloaf but we never observed this at Red Tarns. Overall, we observed kea eating six of the 19 seed species recorded in kea faeces (see below).

Table 4.1. Feeding observations for all (non-kea) bird species seen consuming fruit[c] above the treeline in the fruiting seasons of 2009 and 2010, and for kea in 2010, at Arthurs Pass, Cass, and Mt Sebastapol.

	Number of observations				
Bird species	Fruit	Insects	Other	Published frugivory observations [b]	Fruit spp. eaten (other foods)
Kea (*Nestor notabilis*)	205	2	22	Yes[1,2,3]	Table 4.2
NZ pipit (*Anthus novaeseelandiae*)	3	30	0	No. Mostly insects [4]	*Acrothamnus colensoi, Coprosma perpusilla, Pentachondra pumila*
Silvereye (*Zosterops lateralis*)	2	3	0	Forest plants only [5]	*Coprosma propinqua, Podocarpus nivalis*
Blackbird (*Turdus merula*) [a]	2	2	0	Forest plants only [5]	*Aristotelia fruitcosa, Coprosma propinqua*
NZ falcon (*Falco novaezealandiae*)	1	1	2	Yes [6]	*Leucopogon fraseri,* (lizards, birds)
Tomtit (*Petroica macrocephala*)	1	4	0	Forest plants only [5]	*Coprosma propinqua*
Song thrush (*Turdus philomelos*) [a]	1	3	0	Forest plants only [5]	*Coprosma propinqua*
Canada goose (*Branta canadensis*) [a]	1	0	4		*Coprosma petriei,* (grass)
Chaffinch (*Fringilla coelebs*) [a]	1	2	0	Forest plants only [5]	*Aristotelia fruitcosa*
Rock wren (*Xenicus gilviventrus*)	0	1	0	Yes [7]	

[a] Exotic species

[b] Source: 1 = Clarke 1970; 2 = Campbell 1976; 3 = Brejaart 1988; 4 = Garrick 1981; 5 = O'Donnell & Dilks 1994; 6 = Young & Bell 2010; 7 = Michelson-Heath & Gaze 2007.

[c] Six bird species were seen eating other food items: Harrier (*Circus approximans*) 7 observations on carrion; Grey Warbler (*Gerygone igata*) 2 on insects; Black-back gull (*Larus dominicanus*) 3 on carrion; Skylark (*Alauda arvensis*) [a] 4 on insects; Magpie (*Gymnorhina tibicen*) [a] 1 on insects and 2 on carrion; Chukar (*Alectoris chukar*) [a] 1 on grass seed.

Table 4.2 Relative abundance of fruit available in relation to amount eaten by kea throughout the fruiting season and selectivity ratio (SR) using Ivlev's electivity index (E). (S) selected—those plant species eaten more than expected from their availability (E > 0.3); (N) not selected—those plant species eaten in proportion to their availability; (A) avoided—those plant species eaten less than expected based on their availability (E < -0.3).

Plant species	Early season			Mid season			Late season		
RED TARNS	% fruit available	% of time feeding	SR	% fruit available	% of time feeding	SR	% fruit available	% of time feeding	SR
Phyllocladus alpinus	0	4	S	0	12	S	0	0	-
Muehlenbeckia axillaris	1	0	A	1	29	S	2	0	A
Podocarpus nivalis	46	92	S	57	49	N	70	0	A
Gaultheria depressa	20	0	A	13	9	N	0	0	-
Leucopogon fraseri	2	0	A	2	1	A	7	0	A
Aristotelia fruticosa	2	0	A	0	0	-	0	0	-
Coprosma parviflora	1	0	A	1	0	A	4	0	A
Pentachondra pumila	29	0	A	27	0	A	16	0	A
Acrothamnus colensoi	0	0	-	0	0	-	0	0	-
Gaultheria crassa	na	4	na	0	0	-	0	0	-
SUGARLOAF									
Podocarpus nivalis	48	67	N	51	100	S	na	0	
Pentachondra pumila	11	32	S	7	0	A	na	0	
Gaultheria depressa	32	1	A	31	0	A	na	0	
Acrothamnus colensoi	7	0	A	8	0	A	na	0	
Leucopogon fraseri	1	0	A	2	0	A	na	0	
Muehlenbeckia axillaris	1	0	A	1	0	A	na	0	
Aristotelia fruticosa	0	0	-	0	0	-	na	0	
Coprosma parviflora	0	0	-	0	0	-	na	0	
Gaultheria crassa	0	0	-	0	0	-	na	0	
Phyllocladus alpinus	na	0	-	na	0	-	na	0	

Other bird species were either typically observed feeding on food items other than fruit and/or were rarely seen above the treeline. We observed only eight other native and seven introduced bird species (collectively referred to as "other birds"), which ate relatively little fruit compared with kea (Table 4.1). Just 12 fruit-feeding events on eight different plant species were seen across all other bird species combined, compared with 205 observations for kea (i.e. kea provided 89.5% of all fruit-feeding observations).

Food choice in relation to availability

Relative fruit abundance changed throughout the fruiting season and peak fruiting time differed depending on species and site (Table 4.2). At both sites, all feeding observations took place early and mid season; no kea were seen feeding on fruit late in the season, despite the abundance of ripe fruit in many species. Fruit abundance was not measured during late season at Sugarloaf due to early snowfall. Kea preferred fruits of *P. nivalis*, *P. alpinus*, *Muehlenbeckia axillaris* and *P. pumila*. All other fruiting species were eaten less often than expected at both sites, though the faecal samples showed that 19 species in total were occasionally fed on by kea (see below).

Seed treatment, faecal sampling and gut-passage times

We collected 35 faecal samples in total from other birds. Most (58%) contained insects and 91.4% also contained seeds from a total of 15 different plant species (Table 4.3). The average number of seeds per sample, irrespective of plant species, was 22.7 (±8.7 se), but most samples (65.7%) contained fewer than 20 seeds each. *Coprosma propinqua* was by far the most commonly eaten fruit, with 74.3% of faecal samples containing at least one *C. propinqua* seed. Seeds of *Gaultheria depressa* - the next most abundant species in the faeces - were found in just 14.3% of faecal samples, and were only abundant in one sample (260 seeds ≈ one fruit). Most seeds were intact, with generally low proportions of seed fragments found overall (Table 4.3). Overall, small birds were dispersing seeds intact, but in relatively low numbers and from fewer plant species compared with kea.

Seeds and undigested fruit pulp comprised most of the kea faecal content, with few invertebrates or plant foliage present. We recorded three times more fruiting species in kea faeces (n = 19, Table 4.3) than during our feeding observations (n = 6, Figure 4.1). For example, various *Coprosma* species and *Acrothamnus colensoi* were very common throughout the faecal samples, even though none were eaten during our observations. Overall, we found extremely low proportions of seed fragments in kea faecal samples, and for most plant species 100% of seeds

were excreted intact. Only six of the 19 seed species from kea faecal samples contained some fragments, and all but one species still had at least 96% of the seeds visually intact. Among the 200 rejected *P. nivalis* fruits, we found that 98% were intact and had not been damaged by the beak during feeding.

Table 4.3 Mean numbers of whole (intact) seeds per faecal sample and percentage intact for seeds found in fecal samples from kea (n = 65) and other birds (n = 35).

	KEA			OTHER BIRDS		
	Whole seeds			Whole seeds		
Plant species	Mean (se)	Total seeds	% intact	Mean (se)	Total seeds	% intact
Acrothamnus colensoi	6.7 (2.2)	437	100	0.8 (0.6)	34	82.4
Androstoma empetrifolia	0	2	100	-	0	-
Aristotelia fruticosa	0.1 (0.1)	9	100	0.1 (0)	5	40
Coprosma cheesemannii	-	0	-	0.8 (0.8)	27	100
Coprosma depressa	1.2 (1.2)	75	100	-	0	-
Coprosma fowerakeri	5 (4.7)	325	100	-	0	-
Coprosma intertexta	2.2 (1.7)	144	100	-	0	-
Coprosma perpusilla	0.5 (0.3)	30	100	-	0	-
Coprosma petriei	2 (1.4)	128	100	0.3 (0.3)	12	100
Coprosma propinqua	2.7 2.7)	177	100	8.2 (2.1)	290	98.6
Coprosma serrulata	0.1 (0.1)	5	100	-	0	-
Coriaria plumosa	0.5 (0.3)	32	96.9	-	0	-
Coriaria sarmentosa	6.1 (2.1)	400	98.8	-	0	-
Corokia cotoneaster	-	0	-	0.3 (0.2)	10	100
Gaultheria depressa	89.5 (36.2)	5817	100	8.3 (7.4)	290	100
Leptocophylla juniperina	0.2 (0.2)	12	100	0.1 (0.1)	3	66.7
Leucopogon fraseri	2.4 (0.7)	158	98.7	0.6 (0.6)	20	100
Muehlenbeckia axillaris	2.3 (0.9)	149	98.7	1.3 (1.3)	46	100
Pimelea sericiovillosa	0.1 (.0.1)	7	71.4	-	0	-
Podocarpus nivalis	3.3 (0.2)	219	99.1	0.2 (0.2)	8	100
Pseudopanax colensoi	0.2 (0.2)	11	100	0.1 (0.1)	5	100
Unidentified sp. A	-	0	-	0	1	0
Unidentified sp. B	-	0	-	0.7 (0.7)	24	95.8
Unidentified sp. C	-	0	-	0.5 (0.5)	18	94.4
Unidentified sp. D	-	0	-	0.1 (0.1)	2	100
		8137			795	

Captive kea readily ate blueberries and each bird ate 20 to 30 fruit over a half hour time period. We recovered 33 faeces in total from the 6 birds and counted between 0 and 220 seeds

per sample. Gut passage times for blueberry seeds ranged from 85 to 275 minutes (Figure 4.2) with an overall mean seed retention time of 140.4 ± 36.3 minutes.

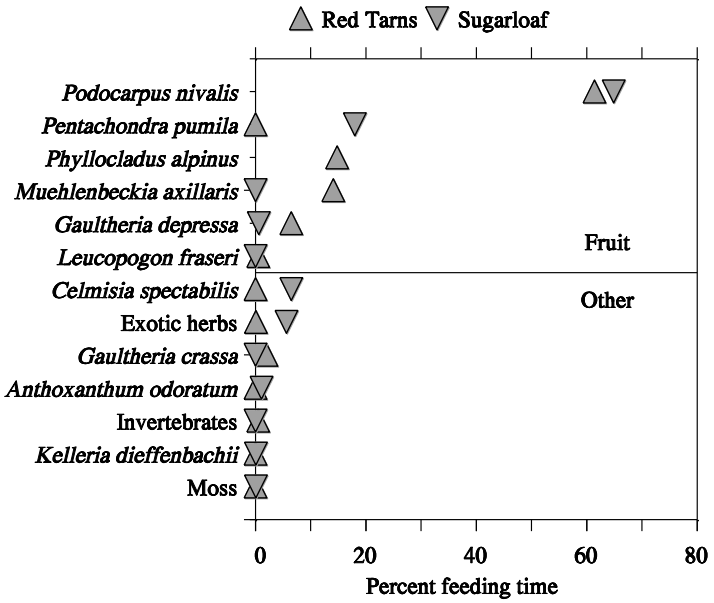

Figure 4.1 Percentage of time kea spent feeding on fleshy fruited plant species and other non-fruit food items (leaves, dry seed capsules and/or flowers of other plants). Exotic herbs were *Taraxicum* sp. and *Pilosella* sp.; *P. alpinus* was not present at Sugarloaf.

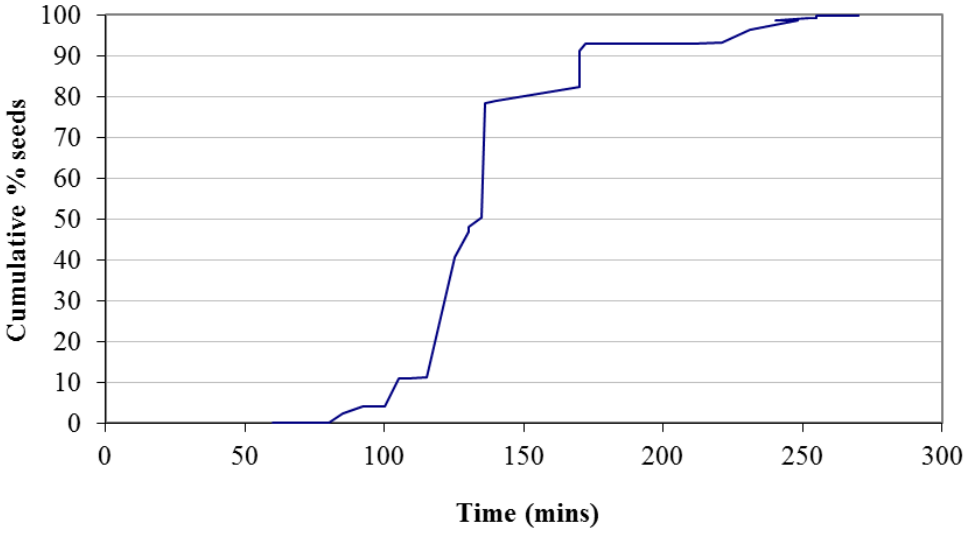

Figure 4.2 Cumulative percentage excretion over time (minutes after fruit consumption) of blueberry seeds passing through 33 faeces collected from 6 captive kea at Willowbank Wildlife Reserve, New Zealand.

Discussion

Our data show that not only are kea legitimate seed dispersers, as previously reported by Clarke (1970), but also they are the numerically dominant avian seed disperser for most fruiting species in New Zealand alpine ecosystems. Kea damaged unexpectedly few seeds during feeding and gut-passage. The passage of seeds through the digestive tract is important in determining their future germination behaviour (Traveset et al., 2001) and reproduction ability. Seed dispersal quantity depends on the number of visits a disperser makes and the number of seeds dispersed per visit, while dispersal quality depends on the treatment of seeds in the disperser's mouth and gut and on seed deposition patterns (Schupp, 1993). Our data showed most seeds were defecated intact. Clarke (1970) collected seeds of five species from kea faeces and most of these germinated, but more germination studies on a greater range of alpine plant species are needed to test the effects of kea gut-passage. We have set up germination experiments, but the results are not yet available, as many New Zealand alpine plant species take years to germinate (both for bird-dispersed and hand-collected seeds). To date after 19 months, only *Coprosma propinqua* has had substantial germination, with kea-dispersed seeds germinating well compared with hand-cleaned seeds and seeds inside whole fruit (30%, 45% and 35% respectively). In general, since scarification effects of gut passage on germination are usually relatively small (Robertson et al., 2006), we would expect intact seeds to germinate well after they have passed through a kea gut.

We observed kea feeding on only one third of the total number of fruiting species found in their faeces. This may reflect the clear preferences by kea for certain fruits, resulting in higher chances of observing kea feeding on these species (e.g. *P. nivalis*). In other studies kea are reported as feeding on fruits of c. 30 fleshy-fruited species (Clarke, 1970; Jackson, 1960; Brejaart, 1988), which – if those seeds are also passed intact – would suggest that kea are likely responsible for the long-distance movement of seed for many more species than we report here.

Work elsewhere shows that animals which eat a small fraction of the seed crop, but have long gut passage times and high mobility, can be very important for long-distance dispersal (Jordano et al., 2007). Kea are the only bird in the New Zealand alpine zone capable of long-distance flights, (Clarke, 1970; Elliott and Kemp, 2004) and have relatively long gut passage times (over 2 hours, see results). Kea are thus more likely to disperse seeds longer distances than small passerines, which typically defecate seeds within an hour of ingestion (Murphy et al. 1993, Jordano et al., 2007), often within 20 minutes (Levey, 1987). Coupled with a long retention time, the frequent long-distance flights made by kea suggest that they are probably the most important long-distance seed disperser of alpine plants. While kea did not disperse all seeds away from the

parent plant (e.g. *P. nivalis*) almost all rejected seeds remained intact, permitting secondary dispersal through other means, such as wind or water.

Given the paucity of bird species in New Zealand's alpine habitat, it is not surprising that we saw so little feeding activity by birds other than kea. Most of the seeds that small birds excreted were from lower-altitude (montane-subalpine) shrub species, some of which also grow beneath the forest canopy (e.g. *C. propinqua*, *Aristotelia fruticosa*). Most low-statured, higher-altitude fruiting species were eaten only by kea. Only one other bird species – the endangered rock wren (*Xenicus gilviventrus*) – lives and breeds exclusively in the alpine zone. While fruits are reported occasionally in rock wren diets (Heather and Robertson, 1996) the distances they move seed is probably limited, as they are poor fliers (Michelsen-Heath and Gaze, 2007). A similar problem besets the New Zealand pipit (*Anthus novaeseelandiae*), which in our data is the next most important seed disperser after kea, but probably only for localised dispersal events. Other small forest-dwelling passerines (e.g. tomtit, *Petroica macrocephala*) sometimes feed on fruits above treeline, but feeding visits are likely to be restricted to lower subalpine elevations and therefore probably contribute little to seed dispersal of alpine plants. A rare report of direct frugivory by the New Zealand falcon (*Falco novaeseelandiae*) – a high-country transient – was reported by Young and Bell (2010). While probably uncommon for New Zealand falcons, several overseas examples demonstrate the important contribution by birds of prey to occasional long-distance seed dispersal events through both direct and secondary seed ingestion (Boehning-Gaese et al., 1999; Galetti and Guimarães Jr, 2004; Padilla and Nogales, 2009).

Non-avian fauna may also contribute to alpine seed dispersal, although data are scarce. Lizards provide effective local dispersal of lowland shrubs on offshore islands – in New Zealand (Wotton, 2002) and elsewhere (Olesen and Valido 2003) – but because of introduced predators lizard density over much of New Zealand is now low, including around Sugarloaf where their role in dispersal of alpine plants was found to be small (Lawrence, 1997). Weta (Orthoptera) can disperse small-seeded native plants over short distances in forests (Duthie et al., 2006) although Wyman et al. (2011) found that most seeds were destroyed in the process. Alpine grasshoppers (L.M.Y. unpubl. data) and scree weta (Larsen and Burns, in press) also disperse tiny seeds of alpine *Gaultheria* species over short distances. Finally, there are a number of introduced mammals in the New Zealand alpine, including possums (*Trichosaurus vulpecula*), red deer (*Cervus elaphus*) and chamois (*Rupicapra rupicapra*) which might eat fruit and disperse some seed, but little is yet known about seed dispersal by larger mammals in New Zealand (Kelly et al., 2010).

Overall, these alpine habitats host a depauperate avian frugivore community despite having many fleshy-fruited plant species, raising evolutionary questions about why this may be so. Some extinct avifauna are likely to have been important for dispersal of alpine plants. Seeds from montane fleshy-fruited plants have been found in gizzards (Burrows, 1989) and coprolites (Wood et al., 2008) of extinct moa species, and while less is known about the diets of upland moa species, they may also have played a role in long-distance dispersal events if seeds were defecated intact. Horrocks et al., (2008) analysed coprolites of kakapo (*Strigops habroptilus*) – a previously widespread but now critically endangered flightless parrot – and reported seeds from six alpine fleshy-fruited species passed through the gut relatively undamaged. Best (1984) also recorded kakapo feeding on fruits and seeds from alpine plants. Moa and kakapo were historically widespread and could have been important frugivores, making their total and near-extinction (respectively) all the more unfortunate.

The seed-dispersal potential of kea is rather unusual. Parrots are typically significant predators of seed because they feed on the embryo of the fruits they forage on (Collar, 1997), and consequently rarely act as primary seed dispersers (Boyes and Perrin, 2010; Janzen, 1981; Jordano, 1983; Galetti and Rodrigues, 1992). The few seeds that are dispersed after gut-passage are tiny (e.g. neotropical *Ficus* and *Cecropia*) (Janzen, 1981). We know of only two other cases of parrots acting as dispersal agents. Boehning-Gaese et al. (1999) showed that a small proportion of seeds of the Malagasy tree (*Commiphora guillaumini*) handled by the Lesser Vasa Parrot (*Coracopsis nigra*) were carried away from the parent, with resulting higher establishment success as seedlings. Sazima (2008) found in Southeastern Brazil the parakeet *Brotogeris tirica* occasionally carried the seeds of the palm *Syagrus romanzoffiana* up to 40 m away from the parent tree. On a global scale, our study demonstrates that kea have unusual feeding behaviour compared with other parrots.

Conservation management and future work

The importance of seed dispersal is being increasingly recognised in conservation management. Seed dispersal helps maintain metapopulation integrity and gene flow between fragmented populations (Hamilton, 1999), such as those on mountain tops. Global warming coupled with anthropogenic habitat modification already poses significant threats to alpine ecosystems (Halloy and Mark, 2003). It is therefore important for long-term plant persistence that dispersal continues to function effectively (Venn and Morgan, 2010). Globally, dispersal failure may be an increasing problem for many plant species (Corlett, 1998; Traveset and Riera,

2005). Although global declines in frugivores may disrupt seed dispersal mutualisms and inhibit plant recruitment, quantifying the likely reduction in plant regeneration is difficult. Seeds that fail to be dispersed may suffer disproportionate mortality beneath parent plants (Janzen-Connell effects) (Janzen, 1970; Connell, 1971). Therefore, dispersal may be required even for local short term persistence. Dwindling kea numbers may negatively affect persistence of fleshy-fruited alpine plant species, especially given the important role of kea in long-distance dispersal events.

Management to maintain seed dispersal mutualisms may be mis-targeted if there is incorrect information about which animals are the most important dispersers. Jordano et al. (2007) showed that in *Prunus mahaleb*, although birds ate most fruits, the largest contribution to long-distance dispersal came from carnivorous mammals. Calvino-Cancela (2002) discovered that gulls, rather than specialist frugivores, were the most effective dispersers in carrying *Corema album* seeds to suitable microsites, while Nogales et al. (1999) demonstrated the quantitative and qualitative effectiveness by common ravens for six plant species in the Canaries. Loss of these key dispersers, especially in fragmented habitats, could impair seed-mediated gene flow and restrict seed arrival to a subset of local microsites.

Across the Northern Hemisphere, bears can act as seed dispersers, and have experienced widespread, historical persecution events for reasons similar to kea persecution – to prevent them from killing livestock (Zedrosser et al., 2011). The difference is that large carnivore populations are now increasing in many parts of Europe and North America through concerted conservation management efforts, even in areas of high human densities. Kea populations are apparently still declining, despite their legal protection since 1986.

The fact that kea were able to ingest fruit and rarely crushed seeds despite their powerful curved 'parrot' beak is noteworthy. These large birds can damage motor vehicles, buildings and signs, yet they can manipulate delicate items with considerable dexterity. This shows the importance of not pre-judging the role of animals within an ecosystem. The morphology of the beak of the kea (or its relation, the kaka (*Nestor meridionalis*), which is an important and at times delicate pollinator (Kelly et al., 2010)) could lead researchers to dismiss kea as likely seed predators.

To conclude, we have identified kea as an unexpectedly important seed disperser species in an ecosystem that may depend largely on this species for long distance dispersal. This is important, as many areas in the Southern Alps have become degraded over time due to high grazing pressure by introduced ungulates, e.g. deer, chamois, tahr (*Hemitragus jemlahicus*) and goats (*Capra hircus*), and also hares (*Lepus europaeus*) and rabbits (*Oryctolagus cuniculus*)

(King, 2005). Maintaining seed dispersal from more intact sites to recovering high country land (after introduced mammals have been controlled) thus helps ensure ongoing plant regeneration. Germination experiments of kea-dispersed seeds and tests for any Janzen-Connell effects on these species in the alpine zone are needed to further evaluate the risk posed by loss of kea. Habitat restoration should also focus on reversing the kea population decline to ensure both the survival of the species and for its role in maintaining vital ecosystem processes.

Appendix

See Appendix 1 for Table A1 and Table A2.

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CHAPTER FIVE

Dispersal effectiveness, germination and establishment in New Zealand montane and alpine fleshy-fruited plants

Whole (left) and cleaned (right) fruits of *Leucopogon fraseri*.
(Photo: L.M. Young)

Abstract

Factors that determine the effectiveness of frugivorous animals as seed dispersers include: effects of gut passage on seed viability and germination, the microsite into which they deposit a seed and their impacts on seedling establishment through herbivory. Differences in behaviour and ecology between frugivores can lead to variation in the spatial deposition of seeds, and consequently alter germination and recruitment patterns for fleshy-fruited plants. I used a manipulative, fully-factorial field experiment measuring: (i) fruit pulp removal (yes/no), (ii) seed deposition microsite characteristics (shade/light), (iii) competition (turf dug/not), and (iv) seedling herbivory (caged/uncaged) to quantify the effects of these seed dispersal qualities on germination, seedling survival and growth. Experiments were followed over 3.5 years for eight montane and subalpine fleshy-fruited species. These species represented a range of families and growth forms that occur naturally in mixed shrub-grassland habitat at Cass near Arthurs Pass National Park, New Zealand. Only three species began to germinate within one year of sowing, while all species experienced at least some germination after 3.5 years. There was a benefit of shade on percent seed germination for the three species that started germinating one year after sowing. Percent seed germination, seedling survival and height growth to 3.5 years was also higher in shaded microsites for seven of the eight species. The magnitude of other effects was smaller, and varied depending on species and stage of recruitment. Animal exclusion cages were less important than shade, with only one species showing significant increases in mean germination and survival. The effects of hand-cleaning seeds were more important in determining how quickly seeds germinated (i.e. germination after one year) rather than determining overall long-term germination success. Germination and survival were largely unaffected by competition, possibly due to vegetation (grass and exotic herbs) regrowth in dug-treatment plots by the time seeds germinated. This study demonstrates the need for long-term experiments to determe the importance of seed dispersal qualities on plant recruitment. Most of these high-altitude species were very slow to germinate and the full germination potential, effects of treatments and microsite on seedling survival and growth of many species may not be realised for a long time period.

Introduction

Processes involved in plant regeneration such as pollination, seed set, seed dispersal in space and time, germination, and survival, are important factors involved in determining spatial patterns in plant communities and can facilitate the maintenance of plant species richness and diversity (Grubb, 1977). Frugivorous animals contribute towards the plant regeneration cycle and the shaping of plant communities through their role in the seed dispersal of fleshy-fruited plants to specific microsites which vary in suitability for germination and establishment (Howe and Smallwood, 1982; Primack and Miao, 1992; Wenny and Levey, 1998; Nathan and Muller-Landau, 2000; Herrera, 2002). However, global declines in frugivorous animals have led to significant reductions in dispersal services for many plant species (Cordeiro and Howe, 2003; Sekercioglu et al., 2004; Sharam et al., 2009; Wotton and Kelly, 2011). There is a need for proper attention to be paid to each stage in the regeneration cycle (Grubb, 1977; Levine and Murrell, 2003) and thus seed-dispersal ecologists should focus efforts on understanding how changes or declines in frugivorous animals mechanistically affects various stages of plant recruitment (Wenny et al., 2011).

Seed dispersal effectiveness has quantitative (number of seeds dispersed) and qualitative (seed treatment, gut passage effects, seed deposition site) components (Schupp, 1993). Each disperser makes different contributions towards dispersal effectiveness for a given plant species depending on the role it plays at each stage in the dispersal process. Knowledge of how frugivores influence dispersal through where they deposit seeds and how far they move seeds, are prerequisite for understanding the influences of post-dispersal processes such as seed predation (Wright et al., 2000; Russo, 2005; Muller-Landau et al., 2008), the microhabitat requirements for germination, establishment (Svenning, 2001) and density-dependent survival (Janzen, 1970; Connell, 1971).

There is a large literature on the importance of microsite characteristics for germination (e.g., Harper et al., 1961; Grubb, 1977; Fowler, 1986; Battaglia and Reid, 1993; Wenney and Levey, 1998). Important microhabitat features include the effects of shade, soil conditions and chemistry, fungal pathogens, temperature, aspect, slope, water availability, timing, competition with conspecific parents, or with other vegetation (Grubb, 1977). Harper et al. (1961) proposed the concept of a “safe site”, a microsite that allows a seed of a given species to germinate and become established. Some seeds may only germinate or establish in shade, others only in light, some in wet microsites, while others may require bare ground or light gaps away from competitors. If seeds of a given species are largely being dispersed to

microsites inappropriate for germination and survival, then the dispersal agent could provide no net benefit for that plant, even if other factors of disperser effectiveness are adequate (e.g. large numbers of seeds dispersed with high proportions intact) (Schupp et al., 2010).

Gut passage may also affect the ability of a seed to germinate (Krefting and Roe, 1949; van der Pijl, 1982; Hererra, 2002; Samuels and Levey, 2005; Robertson et al., 2006), and may influence the rate of germination under a given set of conditions (Traveset, 1998). In a review of ingestion and gut passage by dispersers, Traveset (1998) found that seed dispersers commonly have an effect on the germinability of seeds, the speed of germination, or both, and that gut passage enhanced germination twice as often as it inhibited germination. Moreover, seed germination of shrubs and trees in the temperate zones is more frequently enhanced by gut passage than in the tropics (Travaset, 1998). Seed dispersers can enhance germination in two ways through the direct effects of gut passage: (1) by cleaning the pulp from the seed (deinhibition effect) or (2) by having an abrasive effect on the seed coat and making it more permeable to gases and water (scarification effect). Most studies have failed to differentiate the effects of the deinhibition versus scarification treatments, with most testing the effects of ingested seeds against hand-cleaned seeds, and yet not comparing these against un-dispersed whole fruit (Traveset, 1998; Samuels and Levey, 2005; Robertson et al., 2006). Another problem is that that majority of germination studies have taken place in Petri dishes, often confounding the intended effects (Robertson et al., 2006). Despite a large literature on germination trials, little is known about the likely consequences of dispersal failure in the field (Robertson et al., 2006). Whether gut passage via frugivores really is advantageous to a plant can only be assessed if we also determine the fate of ingested seeds under natural conditions compared to the fate of seeds that have not been ingested (Traveset, 1998).

Increases in germination speed and overall percent of seeds germinated after gut passage are not always necessarily beneficial for the plant. The final outcome (seedling survival and establishment) depends on complex interactions with other factors, such as herbivory (Figuerola and Green, 2004; Campos et al., 2008). Wotton and Kelly (2011) recently showed that dispersal failure reduced regeneration in New Zealand's two largest-seeded tree species through seed predation by introduced mammals, germination and survival of both seeds and seedlings. Factors that are important for germination of seeds may be less relevant for later stages of the plant cycle such as seedling growth, establishment and survival to adulthood (Harper et al., 1965). For instance, a seed of a given species may germinate

better under a certain set of environmental conditions, but require different conditions for establishment and development to adulthood. Optimal conditions for several long-lived forest trees are different between the stages of recruitment. For example, kauri, *Agathis australis*, needs a sparse cover (e.g., of *Leptospermum*) for survival as a seedling, but requires a lack of overhead cover necessary for development in the sapling and pole stages (Beveridge, 1973). Thus it is imperative to carry out long-term studies which monitor the growth and survival of the plant beyond the seedling stage (Schupp et al., 2010).

Finally, exotic species can disrupt seed dispersal processes (Traveset and Riera, 2005). While exotic frugivores can be good seed dispersers for many native plants, they can be detrimental by competing directly with native frugivores, and by modifying the seed shadow and/or germination patterns compared with native dispersers (Traveset and Richardson, 2006; Chapter 3). Most plant communities in New Zealand have likely experienced major changes in the potential disperser fauna since human arrival (Holdaway et al., 2001; Kelly et al., 2010). Many frugivorous birds have decreased in abundance and distribution or become extinct (Holdaway, 1989; Innes et al., 2010), while introduced mammals now outnumber native birds in many areas (Kelly et al., 2010). Birds and mammals are likely to differ in their contribution to seed dispersal, both in quantitative and qualitative effectiveness (Clark et al., 2005; Chapters 3 and 4). Differences in feeding and fruit handling (Howe, 1981), effects of gut passage (Peinetti et al., 1993; Campos et al., 2008), dispersal distance (Jordano et al., 2007), variation in clumpiness of seeds in faeces (Forget et al., 2000) and faecal deposition sites (Martinez et al., 2008: López-Bao and González-Varo., 2011) have been demonstrated to vary broadly among disperser guilds because of different behavioural and ecological traits between them. For example, branches of shrubs and trees provide perching sites for birds where they may defaecate more often, while mammals may deposit more seeds along tracks or pathways where they move along the ground. Birds typically have short gut passage times (< 3 hrs) whereas mammals have much longer ones (> 1 day) (Robertson et al., 2006). Therefore, disparities in seed treatment, gut passage, disperser behaviour and consequently, seed deposition site between original (mostly birds) and novel (exotic mammals) dispersers may differentially affect plant regeneration (Traveset, 1998; López-Bao and González-Varo, 2011).

In this chapter I focus on the individual and interactive effects of gut passage, microsite characteristics including shade and competition, and the effects of seedling herbivory on the germination success, survival and growth of eight New Zealand endemic

montane and subalpine fleshy fruited plant species. Through a factorial field experiment augmented by glasshouse germination studies, I investigated the importance of each of these factors for each stage in the regeneration cycle for each species. In a situation where dispersal services have declined, several predictions about the expected effects of each of these factors on germination success and seedling survival can be made from the literature. One would expect that the effects of gut-passage or hand-cleaning (i.e. fruit pulp removal) would increase percent seed germination, or at least increase the speed of germination. The effects of shade would be expected to vary among plant species, but at least for germination, I would predict that cover and protection from intense sunlight may provide an initial advantage. Competition with other vegetation may negatively affect seed germination and survival, and thus I predict that bare-ground sites will have higher percent seed germination and survival than vegetated sites. Finally, seed predators and seedling herbivores are expected to negatively affect germination and survival, so animal exclusion cages should have a positive effect, particularly for seedling survival.

Methods

Study site and species

Germination experiments were conducted at the Cass Scientific Reserve (43^{o} 2' S, 171^{o} 47' E), Canterbury, New Zealand. Cass is characterised by areas of open high-country grassland (dominated by exotic sweet vernal *Anthoxanthum odoratum*, browntop *Agrostis capillaris*, and native fescue tussock *Festuca novaeseelandiae*), mixed scrub/shrub (dominated by matagouri *Discaria toumatou*, manuka *Leptospermum scoparium*, *Hebe brachysiphon* and shrubby *Coprosma* species), herbaceous and mat plants interspersed with scree, rock and associated vegetation (see Burrows, 1977 and references therein). The highest point is Sugarloaf (1360 m a.s.l.), an isolated mountain peak with a lowered treeline (due to Polynesian and ongoing European burning) and small remnant forest patches ranging in altitude from ca. 650 m to 1250 m a.s.l. At least 35 native fleshy-fruited plant species within ca. 20 genera and 12 families occurred at the site (listed in Young et al., 2012; Chapter 4). Seed dispersal agents included about ten exotic mammal species, several native birds, lizards and invertebrates (see Chapter 3). Eight common fleshy-fruited plant species were selected for germination experiments, representing a range of families, fruit colours, growth forms and habits (Table 5.1). All species have small seeds (0.4-6 mm in length) and fruits vary in size and seed number depending on the species (Table 5.1).

Table 5.1 Characteristics of the eight study species. Fruit and seed sizes are length x width. Codes for fruit colours: R = red, P = pink, W = white, O = Orange, Y = yellow, Bk = black, Pu = purple, Bl = blue. Sources: Mark and Adams (1995); Webb and Simpson (2001).

Family	Species	Fruit colour(s)	Growth form (max height)	Fruit size (mm)	Size of endocarp/ pyrene/seed (mm)	Number of seeds	Diaspore unit
Elaeocarpaceae	*Aristotelia fruticosa*	R,P,W,Bk	Bushy shrub (2m)	4-8 x 4-9	2.0-2.6 x 2.0-2.6	1-3 (avg 1.4)	Drupe with hard endocarp
Ericaceae	*Leucopogon colensoi*	R,P,W	Trailing shrub (40cm)	4-6 x 4-6	2.5-3.5 x 2.2-3	3-5 (-6) filled	Drupe with hard endocarp
	Leucopogon fraseri	O	Prostrate (15cm)	4-6 x 4-6	2.5-4(5) x 2-2.7	2-4 (-5) filled	Drupe with hard endocarp
	Gaultheria depressa	W,P	Low-growing shrub (20cm)	7-13 x 7-12	0.4-0.65	>200	Capsule with accrescent fleshy calyx
Argophyllaceae	*Corokia cotoneaster*	R,O,Y	Bushy shrub (1.5m)	6-8	4.5-6	1	Drupe with hard endocarp
Podocarpaceae	*Podocarpus nivalis*	R,Y	Prostrate, sprawling to semi-erect shrub (2m)	2.5-10	5.5-6.5(-7)	1-2 per receptacle	Seed exarillate with fleshy receptacle
Polygonaceae	*Muehlenbeckia axillaris*	W	Creeping wiry shrub (40cm)	5-7 x 5-7	2.7-3.9 x 1.5-2.0	1	Fleshy perianth surrounding nut

Experimental design

Field seed fate experiment

Seed fates were monitored experimentally using a split-plot full-factorial design with four treatments, each with two levels: (i) in the shade of a shrub versus open grassland with high light levels (shade/light), (ii) whole fruits versus seeds with pulp removed (whole/ cleaned), (iii) competition with grass/mat vegetation versus bare ground (dug/non-dug), and (iv) mammal exclusion versus open access (cage/open-access). Fruit, competition and exclusion (cage) treatments were subplot treatments (eight subplots per replicate) with shade/open being the main-plot treatment (under a shrub, paired with plots 1-3 m away in the open grassland). Cages positions were allocated randomly (using five possible combinations where cages covered four plots at a time across the set of eight, see Figure 5.1). Finally, fruit and competition treatments were randomly allocated within each plot within the cages (light/shade was not randomly assigned) and labelled accordingly. The shrubby species providing shade was kept constant (always *Leptospermum scoparium* for four of the eight species and *Discaria toumatou* for the other four species) while aspect was also kept constant by setting up the experiment to the southeast side of the shrub. Grass and mat vegetation was

also similar between shady and open habitat, and dominated by introduced grasses, herbs such as *Taraxacum* and *Hieracium* species, and native mat-forming *Coprosma petriei* and prostrate *Leucopogon* species. Seeds with pulp removed were always hand-cleaned (rather than via passage through an animal) for consistency. Robertson et al. (2006) showed that, compared with the deinhibition effect of cleaned seeds versus whole fruit, the scarification effect of hand-cleaning seeds versus passage through a bird is relatively small for most species.

Seeds were placed inside 5 cm diameter open-ended tubes of plastic piping (3 mm thick and 7-8 cm tall) wedged into the ground to keep experiments in place (hereafter 'plots'). About 4-5 cm of the tube remained above-ground. Plots were secured by wire pegs, and spaced ca. 2 cm apart (Figure 5.1). Mammal-proof cages (5 mm aperture galvanized steel mesh) were used to exclude all potential seed and seedling predators including lizards and most Orthopterans (e.g. grasshoppers and weta). Cages were secured in place by wire pegs and when seedlings inside cage treatments grew taller than the plots (which were flush with the cages) the cages were raised to avoid interference with seedling growth.

This design was replicated at five independent locations beneath cover shrubs within an area of mixed grassland/shrubland at a montane site at Cass between ca. 600-900 m a.s.l. I aimed to sow roughly the same number of seeds inside each treatment plot for each species, therefore mean seed numbers per fruit was calculated prior to the experiment by sampling >100 fruits for seed number. For *C. propinqua* and *C. petriei*, 10 whole fruits or 20 cleaned seeds (2 seeds per fruit) were placed in each plot. For *L. colensoi, L. fraseri, C. cotoneaster, M. axillaris* and *P. nivalis*, 20 whole fruits or 20 cleaned seeds were placed in each. For *A. fruticosa*, 14 fruits or 20 seeds (mean of 1.4 seeds per fruit) were placed in each, and for *G. depressa*, each fruit capsule consists of at least 200 seeds, so two whole fruits or all seeds from inside two capsules were placed into plots. I sourced all fruits and seeds from a range of fruiting plants at the study site and prepared fruit-pulp removal treatments within a few days of setting up each experiment.

The experiments were set up in early autumn (March-April) 2008 and monitored for 3.5 years until December 2011. I monitored the plots every six months, during winter (around May-June) and summer (December-January), recording number of seeds germinated, cumulative germination, mortality and survival. The assumption was made that a seedling would be unlikely to both germinate and die within any given six month period between measurements. I also measured seedling heights of survivors at the time of final

measurement. Individual seeds and fruits could not be tracked due to their small size and therefore seed predation was not measured in this experiment. The cages were thus used to measure any effects of seedling herbivory by browsers. Seed germination was measured by the appearance of cotyledons above-ground. For the competition treatment (ground dug/non-dug), vegetation was initially removed from within and around plots assigned to that treatment, but continual removal was not done for the 3.5 year experimental duration to avoid disturbing the seeds and interfering with germination processes. Slug bait was added in the initial phases of set up to avoid interference by slugs.

Figure 5.1 Factorial germination experimental setup in shade (left) and open (right) plots at Cass.

Glasshouse germination experiment

Fruits and seeds from the same eight species, plus four extra alpine plant species (*Coriaria sarmentosa* Coriariaceae, *Leptocophylla juniperina, Pentachondra pumila* both Ericaceae, and *Myrsine nummularia* Myrsinaceae) were collected from the field sites and sown in soil trays in a glasshouse. To test the deinhibition effects of dispersal, treatments for all species were simply hand-cleaned seeds versus whole fruits. I monitored germination success, germination rate and seedling emergence for 2.5 years. In addition, defaecated seeds of *C. propinqua* were extracted from bird faeces, and *C. sarmentosa* and *L. colensoi* were extracted from faecal matter of common seed-dispersing mammals (possums and hedgehogs) collected from the field site, and planted alongside the other treatments to test for scarification effects. The glasshouse germination study measured the effect of the hand-cleaning treatment on germination and survival compared with whole fruits in a controlled environment.

Statistical analysis

I analysed data separately for each species and for each phase of recruitment. Response variables for all data analyses were: total seeds germinated at 1 year, 3.5 years, seedling survival to 3.5 years (for germinated seeds) and growth (seedling heights at 3.5 years for the shrub-forming species only). I used linear mixed models (LMMs) to analyse seed germination and seedling survival (with a binomial error distribution with number successes and number of failures as the response variables) and seedling height data (with a gaussian error distribution as a continuous response variable). Germination data was analysed after one year (as well as 3.5 years) because it was initially considered to be a long enough period of time for germination to occur. However, once it became clear that for many of these species, zero percent of seedlings had emerged, it was recognised that a one and 3.5 year comparison of germination would be interesting, and whether patterns of germination and survival would change over this time.

I used the Information-Theoretic Model Comparison (ITMC) approach with multi-model inference, postulating multiple working hypotheses and deriving a set of models which specify quantitative relationships between variables and in different combinations. Models were tested using LMMs because mixed models allow both fixed and random effects to be incorporated in the models. The Information Theoretic approach is favoured because a small number of ecologically relevant variables are defined *a priori* using knowledge of the study system (Burnham and Anderson, 2002). This approach is recommended for making formal model inferences and can provide more meaningful model likelihoods and probabilities using Akaike's Information Criteria (AIC) (Anderson, 2008). Models were developed using the R statistical programme version 2.13.1 (R Development Core Team, 2010) with the packages *lme4* (Bates et al., 2011) and *AICmodavg* (Mazerolle, 2009).

The goal was to compare the ability of multiple hypotheses that consider mechanisms involved in the dispersal process to explain variation in seed germination and survival and growth. Model averaging was not used because I was less interested in prediction than in model comparison, therefore inference was restricted to a subset of all possible models (as suggested by Anderson et al., 2000) and. For germination and survival data, a set of 23 candidate models were specified *a priori* and used to test the relative importance of the models against each other. A set of seven candidate models was specified for growth data. This way, the most important effects could be identified for each response variable. Single-predictor models (including the individual effects of shade, cleaned seeds, competition and

animal-exclusion) and mixed effects models (including combinations of the above predictors and interactions that were hypothesised *a priori* to be biologically important) were compared against a global model and null model (random-effects only). See Appendix 5.1 for the full list of models used to analyse each species for germination, survival and growth data. The experimental factors (outlined above) were specified as fixed effects in the models, while the nesting of plots within blocks was specified as a random effect in all models. The model defined by random effects only was specified as the null model. Random effects models allow separate estimation of a component of variance due to sampling or study design separate from a process variance component (e.g. spatial variation caused by effects other than the experimental treatments). Presented below is the global model used to test against the other candidate models, including all single predictors and interactions between predictors *a priori* deemed to be relevant, for germination (at 1 year and at 3.5 years) and survival.

Germination/survival ~ light + competition + cage + cleaned + shade:competition + shade:cage + shade:cleaned + competition:cage + competition:cleaned + cage:cleaned + (1 | block), family = binomial

The following shows the global model for seedling height data:

Seedling height ~ light + competition + cage + cleaned + (1 | block), family = Gaussian

Model selection based on Akaike's Information Criteria (AICc for second order bias correction) was conducted on the set of candidate models for the germination, survival and growth datasets. Log likelihoods and AICc values were estimated using the *lme4* package (Bates et al., 2011). For each model in the set, AICc was calculated and each model was ranked by rescaling the AICc values. The most parsimonious model was the one with the minimum AICc value and had a value of 0, i.e. $\Delta_i = AICc_i - AICc_{min}$, which estimates the expected distance between the best model and the $_i^{th}$ model. Models for which $\Delta_i \leq 2$ are considered to have substantial support; models with $\Delta_i < 7$ have some empirical support, while those with $\Delta_i \geq$ 10-12 essentially have no empirical support (Burnham and Anderson, 2002). To compare models, Akaike weights (W_i) (normalised likelihood models) were calculated so that values for all models sum to 1. Akaike weights provide an approximate probability for model *i* being the best model and are an ideal way of examining the relative strength of evidence for each model within the set. The higher the value, the more weight is put on the associated model in comparison with the others. Cumulative Akaike weights ($Cum.w_i$) were calculated and models with a ΔAICc of ≤ 2 are presented in the main results. Goodness of fit of the models was evaluated using an adjusted R^2 calculation and these R^2 values are presented for the top models in each set (where AICc values are ≤ 2). Parameter

estimates (using Laplace approximations) of regression coefficients and unconditional standard errors (which incorporate a variance component due to model selection uncertainty; (Burnham and Anderson, 2002)) were calculated and are presented for each predictor variable present in the top model(s) for each set (Appendix A5.2).

Results

Relative germination change and speed over 3.5 years

Seeds from all species germinated within the 3.5 year period of this study; there was no species for which at least some germination did not occur. However, final percent seed germination and germination speed varied substantially depending on species (Figure 5.2). Three species began germination considerably earlier than others: *Coprosma propinqua*, *C. petriei* and *Aristotelia fruticosa* each had at least 5% of all seeds sown germinate within a year. *Leucopogon colensoi*, *L. fraseri*, *Podocarpus nivalis* and *Gaultheria depressa* were particularly slow to germinate with the latter three species not germinating for at least 2.5 years after sowing. Germination in *Corokia cotoneaster* and *L. colensoi* was slow and steady for nearly three years, and then increased at a faster speed after 3 years.

Overall germination success also varied among species. Across all species, mean germination percent was low, with the highest overall mean being 23.2% (*C. propinqua*). The lowest levels of germination were for *G. depressa*, with an overall mean germination of just 0.07% (Figure 5.2). *Podocarpus nivalis* and *L. fraseri* also had very low overall germination, with means of 2.2% and 3.0% respectively at 3.5 years.

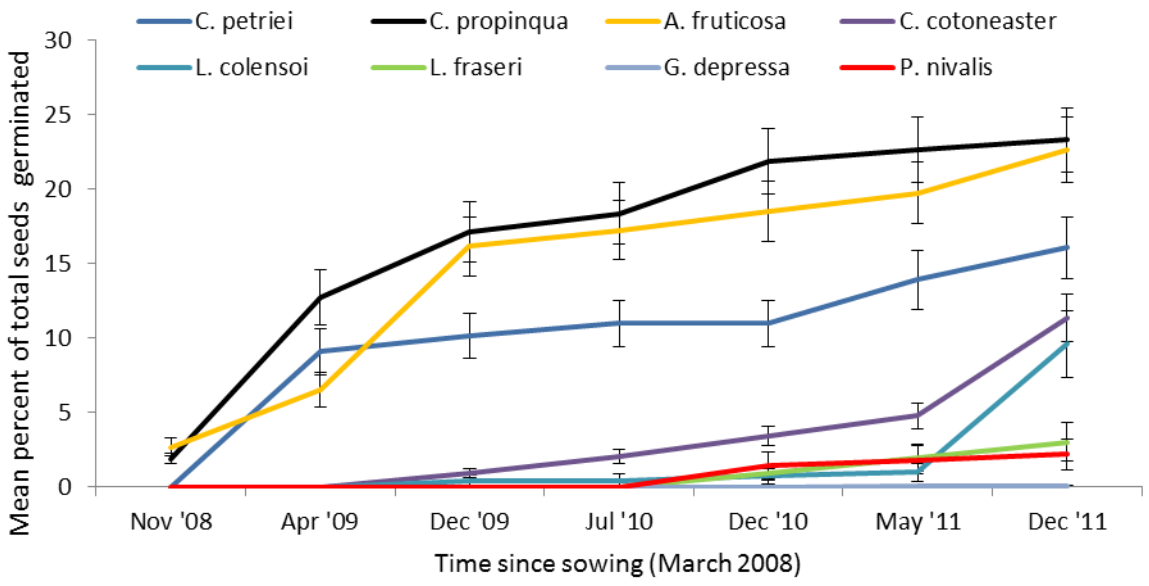


Figure 5.2 Cumulative germination percent over 3.5 years for eight montane and subalpine fleshy-fruited plant species in a full factorial field experiment at Cass, New Zealand. Seeds were sown in March/April 2008. Mean percent germination across all treatments is presented ± standard error.

Germination percentages after one year

Three of the eight species began germinating within one year; *C. propinqua*, *C. petriei* and *A. fruticosa*. In general, mean percent germination was relatively low after one year, with overall means of 1.8% for *C. petriei*, 6.1% for *A. fruticosa* and 12.1% for *C. propinqua* (Table 5.2). Shade and its interactions with other experimental treatments had the biggest effects on percent germination one year after sowing (Tables 5.2 and 5.3).

Table 5.2 Treatment main effects on mean seed germination (± s.e) for the three species that started germinating within one year for fleshy-fruited montane and subalpine plant species at Cass. Values in bold represent biologically meaningful differences between levels within treatments (determined by zero overlap between 95% confidence intervals).

Species	Treatment	Level	% Germination
Coprosma propinqua	Light	Shade	**19.1 ± 2.3**
		Light	**4.9 ± 0.7**
	Fruit	Clean	**15.8 ± 2.1**
		Whole	**8.6 ± 1.5**
	Competition	Dug	13.1 ± 2.2
		Non-dug	10.9 ± 1.5
	Animal exclusion	Cage	**15.5 ± 1.9**
		Open	**8.5 ± 1.7**
Coprosma petriei	Light	Shade	**2.7 ± 0.4**
		Light	**0.9 ± 0.2**
	Fruit	Clean	2.0 ± 0.3
		Whole	1.6 ± 0.3
	Competition	Dug	1.9 ± 0.3
		Non-dug	1.7 ± 0.3
	Animal exclusion	Cage	1.7 ± 0.3
		Open	1.9 ± 0.3
Aristotelia fruticosa	Light	Shade	**10.4 ± 1.4**
		Light	**1.8 ± 0.6**
	Fruit	Clean	7.6 ± 1.4
		Whole	4.5 ± 4.9
	Competition	Dug	6.9 ± 1.3
		Non-dug	5.3 ± 1.1
	Animal exclusion	Cage	**9.0 ± 1.5**
		Open	**3.1 ± 0.7**

Across all three species, plots in shaded microsites had the highest mean percentages of seed germination compared with light plots and other treatment plots (Table 5.2), and consistently appeared as an important predictor variable in all the top models (Table 5.3; see

also Appendix A5.2 for parameter estimates and standard errors for one year germination). The effects of herbivore-exclusion cages were also evident at one year, with a two- and three-fold increase for the shrub species *C. propinqua* and *A. fruticosa*, respectively. The effect of cleaning seeds was also important for *C. propinqua* with mean percent germination after one year nearly twice that of whole (undispersed) seeds (Table 5.2). Model fits were reasonably good for *C. propinqua* and *A. fruticosa* top models (adjusted R^2 values of 0.51 and 0.58 respectively (Table 5.3)).

Table 5.3 Summary results for the binomial linear mixed effects top model(s) used to explain percent germination success after one year in a field study at Cass. A set of 23 *a priori* (linear mixed effects) models was formulated and the best models were selected based upon the Akaike Information Criterion (AICc), with the top models presented here defined as having Δi of ≤ 2. Model terms presented below show all fixed effects predictors and their interactions only (but random effects (block) are included in all models). Adjusted R^2 are presented for the best model only. Abbreviations for the predictors are: L = light/shade; C = cage/open-access; D = Competition (dug/non-dug) and F = fruit cleaned/whole. The 95% confidence set for all candidate models is available from the author upon request.

Species	Model	(Adj R^2)	K[a]	AICc	Δi [c]	Wi [d]	Cum.wi	log($\mathcal{L}$)[b]
Coprosma propinqua	L+C+F	0.51	5	217.1	0	0.28	0.28	-103.1
	L+C+F+D		6	217.2	0.17	0.25	0.53	-102.0
	L+C+F+D:F		7	218.6	1.54	0.13	0.66	-101.5
Coprosma petriei	Global model[†]	0.32	12	264.3	0	0.98	0.98	-117.8
Aristotelia fruticosa	L+C+F+D+L:D	0.58	7	147.9	0	0.64	0.64	-66.2

[a] K - Total number of model parameters including the intercept and residual variance

[b] Log($\mathcal{L}$) – Log likelihood

[c] Δi - Difference between model AICc and minimum AICc value

[d] Wi - Probability of model i being the best in this set of candidate models

[†] Global model contains all single effects terms and all two-way interaction terms between treatments

Germination, seedling survival and growth at 3.5 years

Mean percent germination and seedling survival at 3.5 years were again largely determined by the effects of shade (Table 5.4, 5.5 and 5.6), more so than any other treatment or treatment interactions. For *C. propinqua*, *C. petriei*, *C. cotoneaster*, *L. colensoi*, *G. depressa* and *P. nivalis*, mean percent seed germination was considerably higher in shade compared with light microhabitats, while for *L. fraseri* and *A. fruticosa*, the effects of shade were less important for 3.5 year germination. For *C. propinqua* and *C. cotoneaster*, shade

was highly important right across all stages of recruitment, from germination to seedling survival and growth, always with higher mean successes in shade relative to light plots. The benefits of shade were evident for most other species in varying stages of recruitment (Table 5.4), although effects sizes were usually smaller.

Animal exclusion cages and hand-cleaned fruit treatments also featured in most top models for most species (Table 5.8). Although the effects were not always strong, they were consistently in the predicted directions (Table 5.4). Cage treatments in general resulted in greater means for each recruitment stage than open-access plots, while hand-cleaned fruit treatments gave higher means than whole (undispersed) fruits. While competition usually appeared in top models for germination and seedling survival (Table 5.5, 5.6 and 5.8), it was most likely featuring as a pretending variable. A pretending variable is not biologically important (Table 5.4) but nonetheless appears within a "good" model due to the way AICc is calculated (see Anderson, 2008, pp. 65). For most species and stages of recruitment, there were only small differences between dug and non-dug plots (Table 5.4).

For seedling survival, adjusted R^2 values showing goodness of fit for top models were generally poor in relation to model fits for germination success data (Tables 5.5 and 5.6). This provides us with relatively low levels of confidence in defining which parameters were specifically important for seedling survival (adj. R^2 values ≤ 0.14), but more confidence for specifying which factors determine germination success (adj. R^2 values of 0.27-0.89).

Treatment interaction effects

In general, interactions between treatments were not prevalent across all model sets (Table 5.8), and in just four cases, interactions probably had some degree of biological significance (Figure 5.4). The interaction between competition and fruit treatments was important for 1 year and 3.5 year germination percent for *C. propinqua*, with whole fruits experiencing higher mean percent germination within dug plots (i.e. without competition) than in non-dug plots. For hand-cleaned fruits however, mean percent germination was not different between dug and non-dug plots (Figure 5.4a,b). For *C. petriei*, mean percent germination was higher in shade plots than light plots in general, but this had a stronger effect in non-competitive (dug) shady plots, with a ca. 20% increase in germination compared with non-dug shady plots (Figure 5.4c). For *C. cotoneaster*, shade had a greater effect on mean percent germination in animal exclusion cage plots than in open-access plots, with greater

increases in mean germination at 3.5 years between light and shade in caged treatment plots (Figure 5.4d). For all interaction plots see Appendix A5.3.

Table 5.4 Effects of treatments on mean (± s.e) percent seed germination, percent seedling survival and growth (seedling height) after 3.5 years for eight fleshy-fruited montane and subalpine plant species at Cass. Values in bold represent significant differences (non-overlapping 95% confidence intervals) between levels within treatments (determined by zero overlap between 95% confidence interval bars). NA means height growth was not measured for those species.

Species	Treatment	Level	% Germination	% Survival	Seedling heights (cm)
Coprosma propinqua	Light	Shade	**31.1 ± 1.4**	**55.3 ± 3.1**	**3.4 ± 0.1**
		Light	**15.3 ± 2.5**	**20.5 ± 2.6**	**2.2 ± 0.1**
	Fruit	Clean	26.3 ± 2.4	36.3 ± 3.3	3.1 ± 0.1
		Whole	20.1 ± 1.8	42.7 ± 3.6	2.9 ± 0.1
	Competition	Dug	24 ± 2.3	41.7 ± 3.7	3.0 ± 0.1
		Non-dug	22.4 ± 2.1	36.9 ± 3.2	3.0 ± 0.1
	Animal exclusion	Cage	**28.1 ±2.3**	42.2 ± 3.3	2.9 ± 0.1
		Open	**18.2 ± 1.9**	36.1 ± 3.6	3.1 ± 0.1
Coprosma petriei	Light	Shade	**23.5 ± 2.4**	30.4 ± 3.2	NA
		Light	**8.3 ± 1.2**	29.0 ± 4.3	NA
	Fruit	Clean	18.3 ± 2.2	**37.0 ± 3.7**	NA
		Whole	13.5 ± 1.9	**22.3 ± 3.5**	NA
	Competition	Dug	15.9 ± 2.1	33.4 ± 4.0	NA
		Non-dug	15.9 ± 2.1	26.1 ± 3.2	NA
	Animal exclusion	Cage	14.5 ± 2.1	32.2 ± 4.0	NA
		Open	17.3 ± 2.1	27.7 ± 3.3	NA
Aristotelia fruticosa	Light	Shade	25.2 ± 2.9	33.3 ± 4.9	**5.9 ± 0.1**
		Light	24.2 ± 2.3	30.4 ± 4.1	**1.2 ± 0.4**
	Fruit	Clean	26.5 ± 2.7	31.9 ± 4.3	3.1 ± 0.4
		Whole	22.6 ± 2.2	30.9 ± 4.5	2.1 ± 0.3
	Competition	Dug	25.3 ± 2.3	31.3 ± 4.1	3.0 ± 0.4
		Non-dug	23.8 ± 2.7	31.5 ± 4.7	2.2 ± 0.2
	Animal exclusion	Cage	29.1 ± 3.0	30.1 ± 4.6	2.8 ± 0.4
		Open	20.5 ± 1.9	32.6 ± 4.2	2.5 ± 0.3
Corokia cotoneaster	Light	Shade	**18.5 ± 1.8**	**97.4 ± 1.2**	**3.4 ± 0.1**
		Light	**4.3 ± 0.8**	**87.5 ± 3.8**	**2.1 ± 0.1**
	Fruit	Clean	12.9 ± 1.6	96. 2 ± 2.2	3.2 ± 0.1
		Whole	9.9 ± 1.6	91.7 ± 2.7	2.9 ± 0.1
	Competition	Dug	10.8 ± 1.7	98.3 ± 0.8	3.0 ± 0.1
		Non-dug	12.0 ± 1.5	91.1 ± 3.1	3.1 ± 0.1
	Animal exclusion	Cage	14.4 ± 1.8	98.1 ± 1.1	3.2 ± 0.1
		Open	8.4 ± 1.3	89.4 ± 3.3	2.8 ± 0.1
Leucopogon colensoi	Light	Shade	**14.5 ± 1.9**	95.9 ± 1.5	NA
		Light	**4.8 ± 1.1**	100	NA

	Fruit	Clean	9.5 ± 1.5	99.3 ± 0.3	NA
		Whole	9.7 ± 1.7	95.2 ± 1.7	NA
	Competition	Dug	8.0 ± 1.5	94.5 ± 1.8	NA
		Non-dug	11.2 ± 1.7	100	NA
	Animal exclusion	Cage	11.0 ± 1.7	94.7 ± 1.7	NA
		Open	8.2 ± 1.5	100	NA
Leucopogon fraseri	Light	Shade	1.9 ± 0.6	100	NA
		Light	3.8 ± 1.2	80 ± 5.3	NA
	Fruit	Clean	4.8 ± 1.4	88.9 ± 4.2	NA
		Whole	1.3 ± 0.4	83.3 ± 5.1	NA
	Competition	Dug	3.9 ± 1.3	100	NA
		Non-dug	2.2 ± 0.6	75 ± 5.8	NA
	Animal exclusion	Cage	2.5 ± 0.8	85.7 ± 4.7	NA
		Open	3.6 ± 1.2	87.5 ± 4.4	NA
Gaultheria depressa	Light	Shade	0.1 ± 0.01	94.1 ± 2.7	NA
		Light	0.05 ± 0.01	85.7 ± 4.2	NA
	Fruit	Clean	0.06 ± 0.01	100	NA
		Whole	0.09 ± 0.01	84.6 ± 4.2	NA
	Competition	Dug	0.06 ± 0.02	100	NA
		Non-dug	0.1 ± 0.02	86.7 ± 3.9	NA
	Animal exclusion	Cage	0.09 ± 0.02	91.7 ± 3.2	NA
		Open	0.07 ± 0.01	91.7 ± 3.2	NA
Podocarpus nivalis	Light	Shade	3.8 ± 1.4	95.2 ± 1.4	NA
		Light	0.6 ± 0.2	100	NA
	Fruit	Clean	2.5 ± 0.6	96.3 ± 1.2	NA
		Whole	1.9 ± 1.3	100	NA
	Competition	Dug	3.3 ± 1.4	94.4 ± 1.5	NA
		Non-dug	1.0 ± 0.4	100	NA
	Animal exclusion	Cage	1.3 ± 0.4	100	NA
		Open	3.1 ± 1.4	93.3 ± 1.6	NA

Table 5.5 Summary results for the binomial linear mixed effects top model(s) (Δi of ≤ 2) used to explain percentage of seed germination at 3.5 years in a field study at Cass. Terms and abbreviations are as for Table 5.3.

	Model	(Adj R^2)	K[a]	AICc	Δi [c]	Wi [d]	Cum.wi	log($\mathcal{L}$)[b]
Coprosma propinqua	L+C+F+D:F	0.35	7	258.02	0	0.47	0.47	-121.2
	L+C+F		5	259.44	1.4	0.23	0.71	-124.3
Coprosma petriei	L+C+D+F+L:D	0.38	7	318.1	0	0.56	0.56	-151.3
Aristotelia fruticosa	L+F	0.18	4	8595.5	0	0.58	0.58	-4293.7
	D		5	8596.9	1.39	0.29	0.88	-4293.3
Corokia cotoneaster	L+D+C+F+C:F +L:F+L:C+L:D	0.44	10	208.2	0	0.44	0.44	-92.5
	L+D+C+F+L:C		7	209.9	1.8	0.18	0.62	-97.2
Leucopogon colensoi	L+D+C	0.34	5	486.5	0	0.34	0.34	-238.0
	L+D+C+F+L:C		7	486.9	0.33	0.29	0.63	-236.0
Leucopogon fraseri	L+D+C+F+L:C	0.75	7	93.5	0	0.78	0.78	-38.7
Gaultheria depressa	L	0.27	3	87.5	0	0.14	0.14	-40.6
	L+D		4	87.6	0.003	0.14	0.27	-39.5
	L+F		4	88.4	0.89	0.09	0.36	-39.9
	L+D:F		5	88.5	0.95	0.09	0.45	-38.8
	L+C		4	89.1	1.54	0.06	0.51	-40.3
	L+D+C		5	89.2	1.60	0.06	0.58	-39.2
Podocarpus nivalis	Global model[†]	0.89	12	66.6	0	0.82	0.82	-18.99

[a] K - Total number of model parameters including the intercept and residual variance

[b] Log($\mathcal{L}$) – Log likelihood

[c] Δi - Difference between model AICc and minimum AICc value

[d] Wi - Probability of model i being the best in this set of candidate models

[†] Global model contains all single effects terms and all two-way interaction terms between treatments

Table 5.6 Summary results for the binomial linear mixed effects top model(s) (Δi of ≤ 2) used to explain percent seedling survival to 3.5 years in a field study at Cass. Terms and abbreviations are as for Table 5.3. There were too few seedlings to run models for *L. colensoi* and *P. nivalis*.

Species	Model	(Adj R^2)	K[a]	AICc	Δi [c]	Wi [d]	Cum.wi	log($\mathcal{L}$)[b]
Coprosma propinqua	L	0.17	3	62.8	0	0.32	0.32	-28.2
	L+D		4	64.3	1.46	0.15	0.47	-27.9
	L+F		4	64.4	1.62	0.14	0.61	-27.9
	L+C		4	64.7	1.88	0.12	0.74	-28.1
Coprosma petriei	F	0.0002	3	52.5	0	0.27	0.27	-23.1
	Null model		2	53.9	1.45	0.13	0.40	-24.9
Aristotelia fruticosa	Null model	0.03	2	46.1	0	0.20	0.20	-21.0
	C		3	46.3	0.14	0.19	0.40	-19.9
	L		3	47.9	1.7	0.09	0.48	-20.7
Corokia cotoneaster	L+C	0.10	4	40.4	0	0.15	0.15	-15.9
	C		3	40.5	0.11	0.14	0.29	-17.1
	L+D+C+F+L:F		7	40.9	0.50	0.11	0.40	-12.7
	L+C+F+D:F		7	41.0	0.60	0.11	0.51	-12.7
	L+C+F		5	41.2	0.83	0.10	0.60	-15.2
	C+F		4	41.6	1.26	0.08	0.68	-16.5
Leucopogon colensoi	L+D+C	0.14	5	23.7	0	0.29	0.29	-6.6
	D+C		4	24.5	0.85	0.19	0.47	-8.1
Leucopogon fraseri								
Gaultheria depressa	L+D+F	0.14	5	16.9	0	0.30	0.30	-3.1
	L+D+F+C		6	17.3	0.34	0.26	0.56	-2.1
	L+D+F+C+L:C		7	18.6	1.68	0.13	0.69	-1.5
Podocarpus nivalis								

[a] K - Total number of model parameters including the intercept and residual variance

[b] Log($\mathcal{L}$) – Log likelihood

[c] Δi - Difference between model AICc and minimum AICc value

[d] Wi - Probability of model i being the best in this set of candidate models

Table 5.7 Summary results for the top models used to explain growth, measured by seedling height after 3.5 years in a field study at Cass. Adjusted R^2 values could not be calculated for these types of models, but all relevant models (with a cum. w*i* of 1) are presented and all effects of light/shade are biologically significant (non-overlapping 95% confidence intervals). Terms and abbreviations are as for Table 5.3.

Species	Model	K[a]	AICc	Δ*i* [c]	W*i* [d]	Cum.w*i*	log(ℒ)[b]
Coprosma propinqua	L	4	149.8	0	0.86	0.86	-70.4
	L+ L:C	6	154.1	4.27	0.10	0.96	-70.1
	L+D+F+C	7	156.0	6.19	0.04	1	-69.8
Aristotelia fruticosa	L	4	129.4	0	0.90	0.90	-59.9
	L+ L:C	6	134.0	4.66	0.09	0.99	-59.2
	L+D+F+C	7	138.2	8.79	0.01	1	-59.5
Corokia cotoneaster	L	4	99.4	0	0.55	0.55	-45.2
	L+ L:C	6	100.8	1.44	0.27	0.82	-43.3
	L+D+F+C	7	101.6	2.29	0.18	1	-42.3

[a] K - Total number of model parameters including the intercept and residual variance

[b] Log(ℒ) – Log likelihood

[c] Δi - Difference between model AICc and minimum AICc value

[d] Wi - Probability of model i being the best in this set of candidate models

Figure 5.3 The striking effects of shade (left) compared with light microhabitat on overall seed germination percent, seedling survival, and seedling size for *Corokia cotoneaster* in a 3.5 year field study at Cass.

Table 5.8 Summary of all treatments and interactions that appeared in final top model(s) (with ΔAICc of ≤ 2) for 1 year percent germination, and 3.5 year percent germination, percent seedling survival and seedling heights, represented by "√". Predicted directions of effects are shown in parentheses below the single-treatment terms. Responses that showed a biologically meaningful effect in the predictied direction (i.e. no overlap between 95% confidence intervals around the means) are signified with "+". Directions of treament interactions with biologically meaningful effects are summarised in the table (but see Figure 4 for more detailed interaction plots). Abbreviations: H = hand-cleaned, W = whole fruit, D = dug (no-competition), N = non-dug (competition), C = cage, O = open-access, L = light, S = shade.

Species	Response	Light (S>L)	Fruit (H>W)	Comp (D>N)	Cage (C>O)	Light : Fruit	Light : Comp	Light : Cage	Comp : Cage	Comp : Fruit	Cage : Fruit
Coprosma propinqua	Germination 1 yr	√ +	√ +		√ +					√ W:D>N	
	Germination 3.5 yrs	√ +	√		√ +					√ W:D>N	
	Survival to 3.5 yrs	√ +	√	√	√						
	Seedling height 3.5 yrs	√ +									
Coprosma petriei	Germination 1 yr	√	√	√	√	√	√	√	√	√	√
	Germination 3.5 yrs	√ +	√	√	√		√ D: S>L				
	Survival 3.5 yrs		√ +								
Aristotelia fruticosa	Germination 1 yr	√ +	√	√	√ +		√				
	Germination 3.5 yrs	√	√	√							
	Survival 3.5 yrs	√			√						
	Seedling height 3.5 yrs	√ +									
Corokia cotoneaster	Germination 3.5 yrs	√ +	√	√	√	√	√	√ C:S>L			√
	Survival 3.5 yrs	√ +	√	√	√	√				√	
	Seedling height 3.5 yrs	√ +						√			
Leucopogon colensoi	Germination 3.5 yrs	√ +	√	√	√			√			
	Survival 3.5 yrs	√		√	√						
Leucopogon fraseri	Germination 3.5 yrs	√	√	√	√			√			
Gaultheria depressa	Germination 3.5 yrs	√	√	√	√		√			√	
	Survival 3.5 yrs	√	√	√	√						
Podocarpus nivalis	Germination 3.5 yrs	√	√	√	√					√	

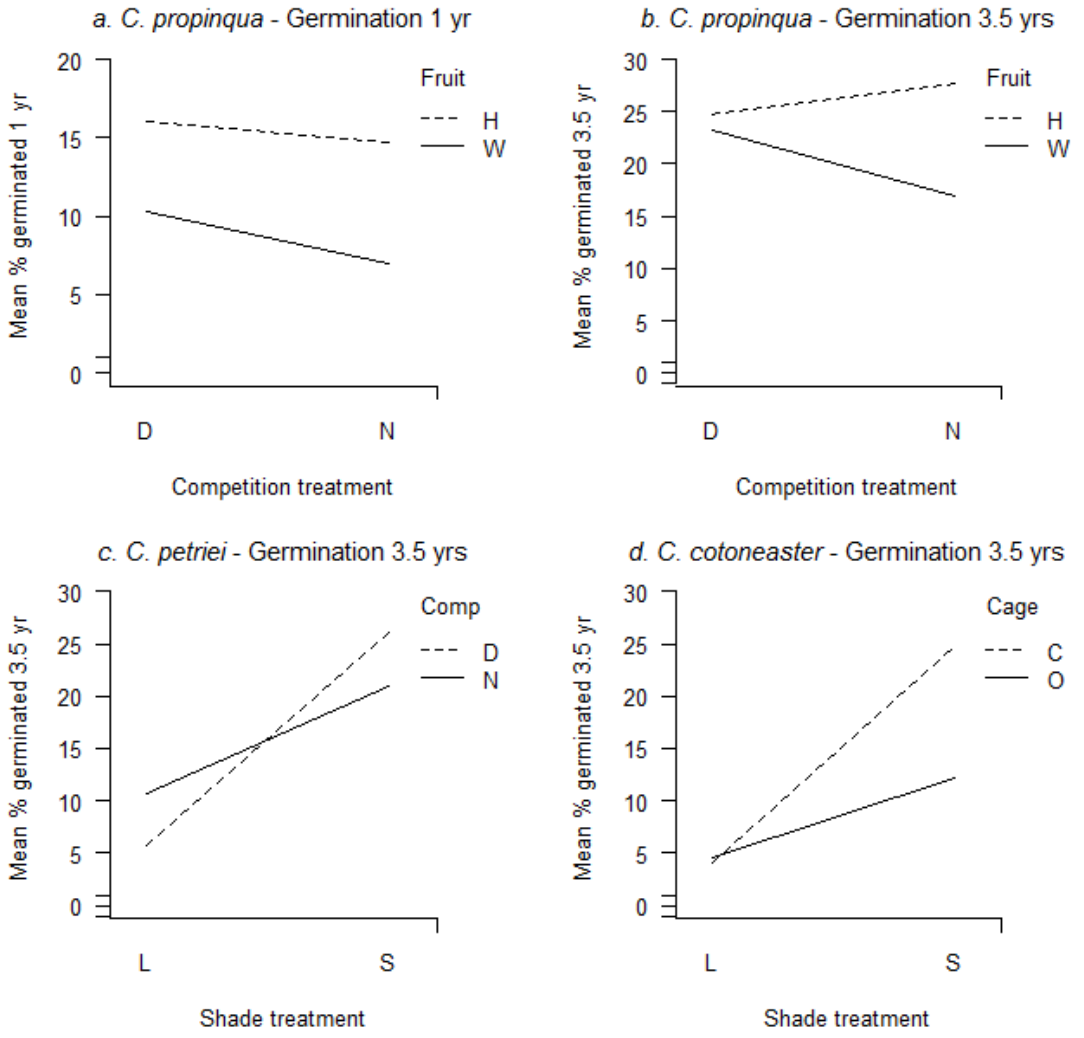


Figure 5.4 Interaction effects from the final top model(s) (with ΔAICc of ≤ 2) that had biologically meaningful effects (Table 5.8). Abbreviations: H = hand-cleaned, W = whole fruit, D = dug (no-competition), N = non-dug (competition), C = cage, O = open-access, L = light, S = shade.

Germination percent, time, and the importance of shady microsites

The importance of a shady versus light microsite was evident across the entire study period for six of the eight study species (Figure 5.5). For the two species for which results indicated that the effects of shade were less important for seed germination (*L. fraseri* and *A. fruticosa*), nearly half of the experimental shade treatment plots were disturbed by pigs after 1.5 years, reducing the power of the analysis. Although the tubes were overturned and unable to be placed back into the correct positions according to the specific treatment combinations for on-going sampling, the experimental seedlings themselves remained largely undamaged at the disturbed plots. Photographs of *A. fruticosa* seedlings showed that in general, seedlings

were more numerous and heights were greater in shady microsites among the paired shade/light blocks, suggesting that there could have been an effect on survival.

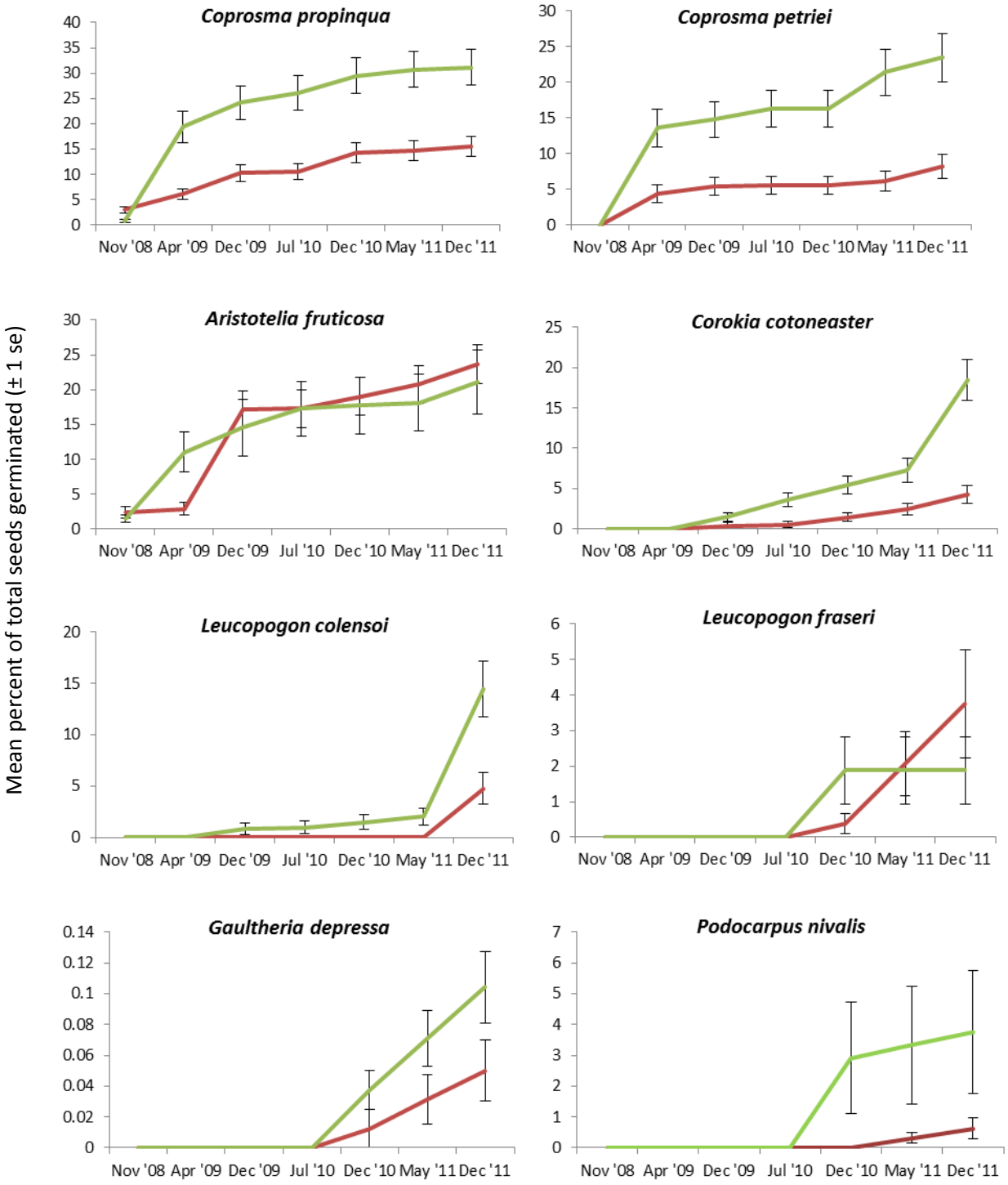


Figure 5.5 Cumulative germination percent over 3.5 years for eight montane and subalpine fleshy-fruited plant species in a full factorial field experiment at Cass, New Zealand. Green lines represent mean germination percent in shade treatment plots and brown lines represent mean (± se) germination percent in light treatment plots. Note differences in scale on the y axes.

Glasshouse 2.5 year germination study

Germination of cleaned and whole fruit

The glasshouse germination study enabled testing of the effects of the hand-cleaning fruit treatment on germination and survival compared with whole fruits under controlled conditions. Total germination percentages at the end of the glasshouse germination study were consistently higher for hand-cleaned compared with whole fruit, except in *C. petriei* (Figure 5.6). For *A. fruticosa* and *M. axillaris*, total germination for hand-cleaned fruit was nearly 20% higher than for whole fruit. Total germination for *C. propinqua* seeds which passed through birds was higher than for both cleaned and whole fruit, but final percent germination between all three treatments was confined to within 10% (Figures 5.6 and 5.7). Mean percent germination across all species for hand-cleaned fruit (48.3%) was significantly higher than for whole fruit (36.9%) treatments ($t_{(1,4)} = -3.06$, $p = 0.037$).

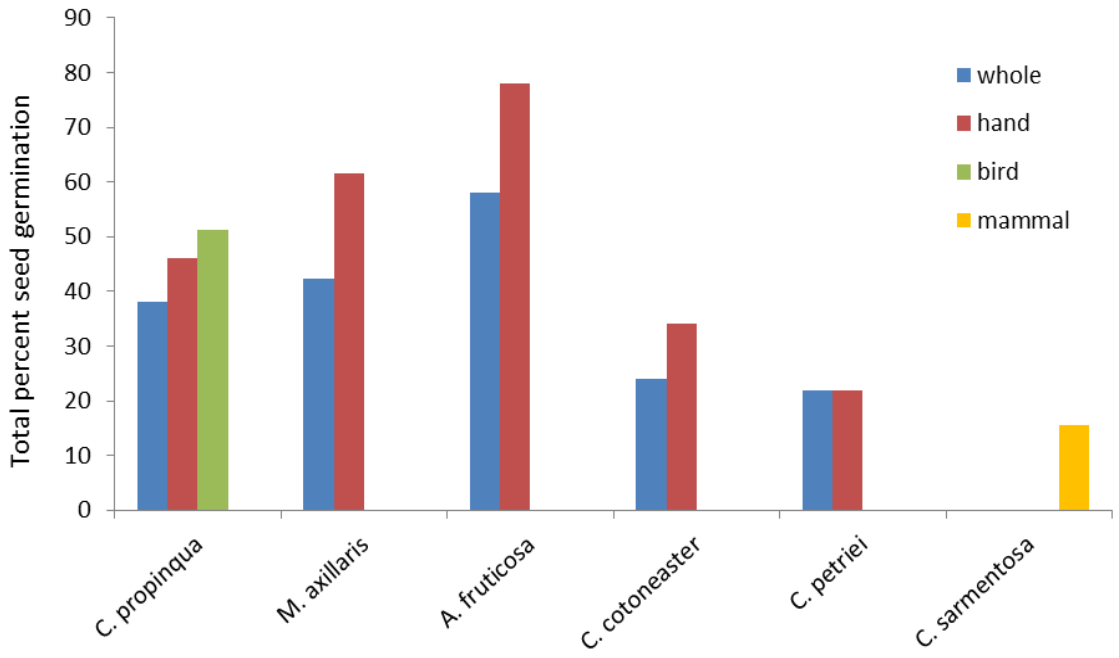


Figure 5.6 Total germination percentages for five montane and subalpine fleshy-fruited plant species in a 2.5 year glasshouse study investigating differences between the following fruit treatments: hand-cleaned, whole and through-birds and mammals. Missing bars indicate that particular treatments were not done for those species.

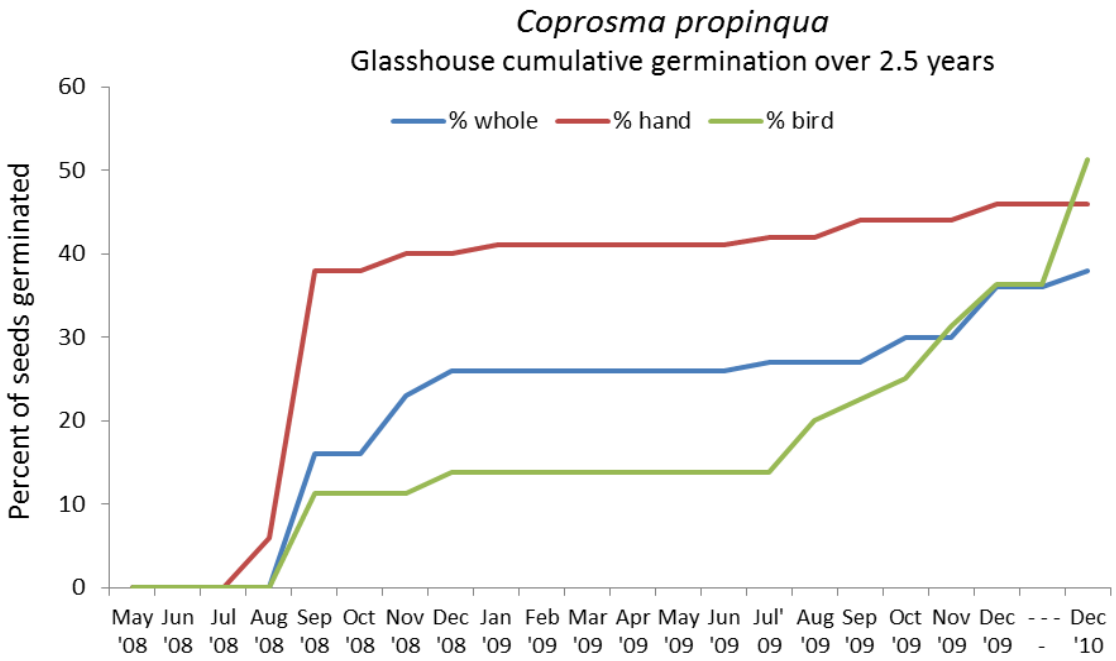


Figure 5.7 Cumulative percent germination in *Coprosma propinqua* comparing whole fruit, hand-cleaned and bird-processed fruit over 2.5 years. Note the break on the right-hand-side of the x-axis between December 2009 and 2010 (where germination was not monitored monthly).

For the other seven species, germination either did not occur at all during the 2.5 year study (*G. depressa*, *P. nivalis* and *P. pumila*) or experienced extremely slow rates of germination and in very low numbers. For *Cyathodes juniperina*, one out of 23 hand-cleaned seeds germinated after eight months (and died within two months). After 2.5 years, four more seeds germinated - two hand-cleaned, two whole (and died within five months). For *L. colensoi*, *L. fraseri* and *Myrsine nummularia*, several seeds germinated nearly two years after sowing (from both treatments) but all died within five months. Of the 200 *C. sarmentosa* seeds extracted from mammal faeces, 15.5% germinated relatively early on (after ca. four months) with only one more seed germinating from each of the four trays at later dates.

Seedling heights

Differences in mean seedling heights between hand-cleaned, bird-processed and whole fruit treatments measured after 1.5 years were not statistically significant for *C. propinqua* (ANOVA: $F_{(2,43)} = 0.78$, $p = 0.46$). There was no significant difference between hand-cleaned and whole fruit treatments for *C. cotoneaster* (t-test: $t_{(1,20)} = -1.21$, $p = 0.12$). For *A. fruticosa* however, mean seedling heights were significantly greater for hand-cleaned compared with whole fruits (t-test: $t_{(1,68)} = -3.31$, $p = 0.0007$), (Figure 5.8).

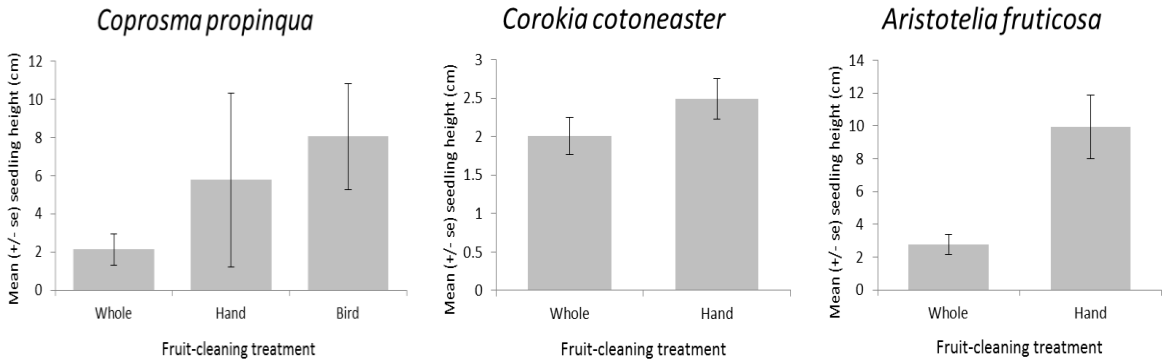


Figure 5.8 Mean seedling heights as measured at 2 years for whole fruit, hand-cleaned and through bird treatments for *Coprosma propinqua*, *Corokia cotoneaster* and *Aristotelia fruticosa* in a glasshouse study.

Figure 5.8 Glasshouse germination experiment showing the strong effects of sowing hand-cleaned (H) seeds compared with whole fruits on seed germination after 6 months (left photo, H = lower half of tray) and seedling height at 2.5 years (right photo, H = left side of tray) in *Aristotelia fruticosa*.

Because the overall effects of shade/light microsites were almost always the most important predictor for each stage of recruitment, estimates of the overall reductions caused by getting into a suboptimal (light) habitat were calculated for each stage (Table 5.9). For *C. propinqua*, *C. cotoneaster*, *C. petriei* and *L. colensoi*, light treatment caused a >50% reduction in germination. Reductions in seedling survival were not as drastic, except for *C. propinqua*. Light had the largest effect on growth for *A. fruticosa* with seedling height growth in light microsites as low as 20% of seedlings in shaded sites. Overall, the multiplicative effect of recruitment and growth in light microsites across five species was only 11-34% of that in shaded microsites (Table 5.9).

Table 5.9 Estimates of the overall effects of getting into a suboptimal (high light) habitat at each stage of recruitment and growth, relative to performance in shady habitat at the same stage. Shown in the last column is the overall reduction in recruitment and growth resulting from growing in light microsites compared with shade. Effects on germination, survival and height growth (where measured) at 3.5 years were calculated using mean percentages in Table 5.4.

Species	Germination	Survival	Height growth	Overall relative performance
Coprosma propinqua	0.49	0.37	0.62	0.11
Corokia cotoneaster	0.23	0.90	0.62	0.13
Aristotelia fruticosa	0.96	0.91	0.20	0.17
Coprosma petriei	0.35	0.95	NA	0.33
Leucopogon colensoi	0.33	1.04	NA	0.34

Discussion

I hypothesised that regeneration would be worse in this experiment for seeds which were not dispersed via gut passage, for seeds deposited to unsuitable microsites for regeneration (high light habitat with vegetative competition), and for seeds/seedlings that were vulnerable to seedling herbivores (not within animal exclusion cages). In this factorial field experiment, I found that recruitment of most species was very dependent on certain microsite conditions, specifically shade. The effects of shade and its associated properties are widely understood to be important factors in determining long-lasting patterns in plant recruitment (Tilman, 1985; Silverton and Tremlett, 1989). In contrast, the effects of removing the fruit flesh, reducing competition by digging up the turf, and protecting plots from herbivores were all less important than I had hypothesized.

The importance of shady microsites for germination, survival and growth

The mechanisms by which shade actually benefit survival of seedlings are probably species-dependent. For the three divaricating shrub species in this study (*A. fruticosa, C. cotoneaster* and *C. propinqua*), the effects of shade were stronger than for any other species, and were seen at all stages of recruitment. Shade was important for seedling survival for *C. propinqua* with 2.5 times more seedlings surviving in shade than light plots. Mean survival of *C. propinqua* seedlings in light plots was just 20% compared with 55% in shade plots. Germination percent in shade plots was 3.5 times greater than light plots and seedling survival increased from 87.5% in light plots to 97.5% in shade plots for *C. cotoneaster*, demonstrating that there were definite shade-related microsite requirements driving recruitment. Seedling height growth was also greater for all three divaricate shrub species in shade plots: the greatest effects were seen in *A. fruticosa* with seedling heights in shade plots around five times greater than in light plots on average. Seedling morphology also differed drastically. Seedlings in light plots were not only shorter and smaller; they were red in colour with anthocyanin pigments, particularly in *A. fruticosa* and *C. cotoneaster*. Seedling biomass, although not measured during this study (to allow ongoing measurements of survival) was also obviously reduced in high light conditions, as most seedlings were no more than several centimetres tall, with very few leaves compared to shade-plots seedlings.

Species should be most vulnerable to photoinhibition near their limits of tolerance to environmental variables; and seedlings, due to their lack of stored resources, should be especially vulnerable to reductions in carbon gain associated with chronic photoinhibition (Ball, 1994). Photoinhibition occurs when light is absorbed by the photosynthetic apparatus in excess of the photosynthetic requirement, leading to a light-dependent decline in photosynthesis (Osmond, 1981). Photoinhibition can be exacerbated by any environmental stresses (e.g., cold temperatures, high light) that limit the capacity of the photosynthetic apparatus to use photon fluxes received (Osmond, 1994). Howell et al. (2002) hypothesised that the leaves of adult plants of these three divaricate shrubs are sensitive to cold-induced photoinhibition and found that by shielding their leaves with an outer screen of branches, they reduce photoinhibition of photosynthesis. Divaricate shrubs are most abundant in exposed, frosty inland habitats in the central South Island of New Zealand (McGlone and Clarkson, 1993; Wilson and Galloway 1993) such as Cass, where they are often exposed to bright sunshine following a cold night - conditions which would promote cold-induced photoinhibition (Howell et al., 2002). Howell et al. (2002) contend that this architectural self-

shading in divaricate plants maximizes potential carbon fixation by minimizing photoinhibition. Solar radiation is lower beneath shrubs compared with high levels in open grassland, especially during summer months, and shrubs offer a protective retreat from frosts compared to open habitat (Nunez and Bowman, 1986; Germino and Smith, 2000), and perhaps seedlings of these divaricating shrubby species experience more protection in these specific microsites.

For the other (non-divaricate) study species, the effects of shade versus light microsites mattered more for germination than for seedling survival. This could possibly be due to the fact all the remaining species (except *C. petriei*) did not begin germinating until at least 2.5 years after sowing, and thus seedling mortality has not yet had sufficient time to become evident. For *L. colensoi*, *G. depressa* and *P. nivalis*, percent seed germination was consistently higher in shade plots than light plots. This suggests that certain abiotic and other ecological variables associated with shade and/or sheltered conditions were important drivers for promoting more rapid seed germination, or greater percent seed germination in general.

Other mechanisms could potentially drive higher germination and recruitment in shady sites. Moisture levels are probably higher in the shaded sites, where seedlings are more likely to be protected from the drying and desiccation compared with the exposed grassland sites. Large areas of the grassland (light) sites (in this study and elsewhere) are now dominated by exotic grass swards (*Agrostis* and *Anthoxanthum*) and invasive hawkweeds (*Hieracium* spp.) which have replaced native grasslands (previously dominated by *Festuca* tussock) due to grazing (Rose et al., 1995) and fire (Wiser et al., 1997). These exotic grasses form dense swards with relatively short canopies, interspersed with often dense mats of *Hieracium*. The exotic-dominated communities are subject to moisture loss (Sessions and Kelly, 2000), offering different canopy cover and microsite conditions for small seedlings. *Festuca* and other native short tussock grassland species (e.g., *Poa* and short *Chionochloa* species) form large individual clumps with low levels of water loss (Ingraham and Mark, 2000). Native tussock-dominated grasslands are therefore likely to provide more sheltered inter-tussock spaces with adequate (and not high) light levels and moisture conditions than exotic grasslands (Sessions and Kelly, 2000). These differences may partly explain why the succession of native shrubland species after fire is limited, and why seed germination and seedling survival is better, at least in early years of growth, beneath existing shrub cover within grasslands.

Effects of competition

Germination and survival appeared to be largely unaffected by vegetative competition for most of the species in this study, both in open grassland and beneath the shade of shrubs. The only exception was for *C. propinqua* for which there was an interactive effect between fruit-cleaning and competition treatments, with higher germination at 1 and 3.5 years of whole (undispersed) fruit in dug (non-competitive) plots than non-dug plots. For cleaned fruit, there was no difference in germination success between dug and non-dug plots. For many species studied overseas, seedling establishment is strongly inhibited by grass because it creates a microclimate unfavourable to the leaves of overwintering evergreen seedlings in frost-prone areas (Ball, 1994). The over-riding influence of shade probably mattered more than competition for most of the species in this study, such that any effects of competition were obscured.

Effects of seed predation and seedling herbivory

Animal-exclusion cages had surprisingly low effects on seedling survival, suggesting that seedling herbivory by animals was not a major problem for the study species at these sites. Cage treatments were important for germination success in *C. cotoneaster*, with a larger proportion of seeds germinating under cages than in open access plots in shady microsites. This suggests that cryptic seed predation in *C. cotoneaster* may have been occurring, probably at low levels. It was not possible to count ungerminated seeds remaining in plots after a year or so without causing disturbance to the study. Whether these lowered rates of germination were due to removal of seeds by predators such as mice or rats, or whether seed-predating invertebrates were destroying seeds inside plots, is unknown. Also unclear is whether seed predators were removing or destroying whole (undispersed) fruits or cleaned seeds, because of the long time period after sowing before this phenomenon was noted.

Effects of fruit pulp removal

This study allowed the importance of fruit pulp removal to be distinguished relative to other factors thought to be instrumental in plant regeneration. Whether gut passage via frugivores really is advantageous to a plant can only be assessed if the fate of ingested seeds is determined under natural conditions compared to the fate of seeds that have not been ingested (Traveset, 1998). I used hand-cleaned fruits as a proxy for frugivore-cleaned fruits as most studies show that this deinhibition effect is similar between the two (see review by

Robertson et al., 2006). Results from the glasshouse study showed that cleaned seeds of *A. fruticosa* and *C. propinqua* began to germinate earlier, (but not necessarily at a faster speed), than seeds from whole (undispersed) fruits. Additionally, final percent germination was higher for hand cleaned fruits in the glasshouse overall.

In a review of gut passage effects on germination, Traveset (1998) found that most studies do not provide data on germination "rate" (i.e. the time elapsed until the first germination and/or the time elapsed until 50% of the seeds have germinated), only measuring the total percentage of seeds that germinated after a given period of time (often just a few months). Birds usually accelerated the rate of germination, but Traveset (1998) proposes that differences in germination rates between dispersed and control seeds are usually only a couple of days or weeks, rarely a few months. In this study, field experiments showed the effects of pulp removal on germination percent at one year were strong for *C. propinqua* only, with mean percent germination for cleaned fruits nearly twice as high compared with whole fruits (8.6% versus 15.8%, Table 5.2). However, this effect disappeared after 3.5 years (Table 5.4) suggesting that germination speed in the field was slower initially for whole fruits, but in the longer-term, pulp removal was less important. This demonstrates the importance of running long-term field studies, as factors deemed important in the short term may not be ecologically relevant in the longer term.

Was germination enhanced by pulp removal overall and how does this compare to other New Zealand plants? It is not easy to conclude whether germination was generally enhanced by pulp removal across the eight study species. Differences in final (3.5 year) percent germination between cleaned and whole fruit treatments were small for most species, suggesting that in general, pulp-removal was probably not important for long-term recruitment. Kelly et al. (2010) also found no long-term evidence for germination failure in whole fruits compared with cleaned seeds. They did find that for large-fruited New Zealand forest species, germination from whole fruits was often also slower than cleaned seeds but similarly, the differences in germination percentages reduced over time. Kelly et al. (2010) conclude that this deinhibition effect in the field for large-seeded New Zealand plants is biologically not very important (in their case the average across ten different species was about a 10% reduction in germination). The difference in my study was somewhat larger – the mean germination percentage from whole fruits across all species (36.9%) was reduced by one-quarter compared to hand-cleaned fruits (48.3%), but even so this reduction is smaller than in earlier experiments done in laboratory conditions.

Are faster rates of germination actually advantageous? Enhanced germination may be more advantageous in less constant environments with unpredictable climatic conditions (Izhaki and Safriel, 1990) such as mountains. Seedling emergence over several years (intermittent or asynchronous germination) is known to be especially important for the survival (persistence) of populations of plants in alpine regions, where fruit set and ripening of seeds are not guaranteed every year (Urbanska and Schütz, 1986; Liebst and Schneller, 2008). The risk of seedling mortality is also spread over a longer period of time (Harper, 1977). Therefore, in these mountain plant communities in New Zealand, delays in germination are also likely to be more advantageous in the long-term. However, where conditions are always favourable (such as in the glasshouse experiment), earlier germination would be expected to confer a size benefit on seedlings, which was observed. Interestingly, in the field experiment where the turf was dug, this would be predicted to provide a benefit to early germination since the dug ground is recolonised by (mostly exotic) perennials. Thus, over time I would have predicted a significant interaction between whole fruit versus hand cleaned, and dug turf versus not. In fact, that particular interaction was rarely important (except for a small increase in mean final percent germination (at 3.5 years) for whole fruits in dug plots compared with non-dug plots for *C. propinqua*, see Figure 5b.)

Complexities of the alpine environment

One of the intriguing findings from this study is just how long these subalpine species took to even begin seedling emergence. *Gaultheria depressa*, for example, is widespread among alpine plant communities. Each fruit possesses hundreds of tiny seeds, yet most seeds failed to germinate within 3.5 years, suggesting either that the specific microsite conditions are perhaps more precise than any covered during this study, or that this species has a very long period of innate seed dormancy. Bet-hedging chances of reaching a site suitable for germination and establishment may be traded off by having large numbers of small seeds rather than few large seeds.

Potential explanations for low germinability of the higher-altitude study species (*G. depressa* and *P. nivalis*) could be that optimal conditions required for germination and establishment were not met. This experiment was conducted in lower-altitude (montane) mixed shrubland/grassland which may not have provided the specific conditions needed for germination. For instance, some species (particularly alpine-adapted species) probably require a temperature cue (usually freezing for alpine plants) or prolonged period of cold,

specific freeze/thaw patterns in the soil, specific soil surface temperatures, microclimate, soil topography and parent material, or seed coat scarification (Nicholls, 1935; Bliss, 1956). In alpine species, dormancy is a long recognized phenomenon. As early as 1913, Braun reported that many alpine species did not germinate at all, even after cold stratification. Certain cues may be needed to break seed dormancy, although these are not yet fully known because of a lack of knowledge on the mechanisms that underlie dormancy in alpine species (Schwienbacher et al., 2011). Also unknown is whether these species are viable after a certain period and how long they can remain dormant. Although this study has begun to understand whether low alpine and montane species need certain microsites and conditions for germination, further work is needed to determine the requirements for higher alpine species. Germination of most of these species was spread over a minimum of 3.5 years, suggesting the formation of a persistent seed bank.

Qualitative aspects of seed dispersal with a changing frugivore fauna

The need to understand how changes or declines in frugivorous animals mechanistically affect various stages of plant recruitment has been realised (Wenny et al., 2011) but little investigated (Wotton and Kelly, 2011). It is difficult to know whether any measures of reduced dispersal services unequivocally demonstrate a cost to plants because the safe sites for plant regeneration are so uncertain in space and time (Kelly et al., 2004), and thus better quantitative measures of dispersal effectiveness are required (Kelly et al., 2010). Disparities in seed treatment, gut passage, disperser behaviour, and consequently, seed deposition sites between native dispersers (mostly birds for New Zealand) and novel dispersers (here, mostly exotic mammals) may differentially affect plant regeneration (Traveset, 1998; López-Bao and González-Varo, 2011). With a changing frugivore fauna across most New Zealand ecosystems, we can expect large changes in the way seed dispersal mutualisms are functioning. This study has identified how varying stages in the process of recruitment are affected by qualitative aspects of dispersal, and now we can relate these to what we know about behavioural and ecological differences between the original and novel dispersal agents. This study was conducted in natural field settings, making it possible to measure the features that were filtering recruitment success at each stage of the multi-step process.

This study provided some insight into which of these effects have been important at each stage of recruitment for eight species, and showed that the shade treatment in particular

had the strongest overall effects on germination among most species, and also on survival and growth of some of them. The behaviours and ecological traits of many of the novel disperser fauna in these montane and alpine plant communities (e.g., possums, sheep, hares, rabbits and hedgehogs) differ from that of the original seed dispersing avifauna. As a consequence, the majority of seeds were dispersed into open, high light grassland habitats and forests unsuitable for establishment of alpine species (Chapter 3) by many of these mammals. Although seed germination and seedling survival appeared to be largely unaffected by the competitive effects of tightly-packed vegetation within the grassland communities, the strong detrimental effects of the high-light habitat to which mammals dispersed most seeds directly demonstrates that introduced mammals are changing the patterns of seed dispersal and recruitment in New Zealand montane and alpine ecosystems.

APPENDIX 5.1 Full list of models

APPENDIX 5.1a List of all models used to test the effects of experimental treatments and their interactions on germination to 1 and 3.5 years and seedling survival to 3.5 years.

The first model is the maximal model
1. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ light + comp + cage + cleaned + light:comp + light:cage + light:cleaned + comp:cage + comp:cleaned + cage:cleaned + (1 | block), family = binomial)
Second model is the NULL model (random effects of block only)
2. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ (1 | block), family = binomial)
Single factor treatments and each paired combination
3. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ light + (1 | block), family = binomial)
4. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ comp + (1 | block), family = binomial)
5. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ cleaned + (1 | block), family = binomial)
6. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ cage + (1 | block), family = binomial)
7. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ light + comp + (1 | block), family = binomial)
8. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ light + cleaned + (1 | block), family = binomial)
9. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ light + cage + (1 | block), family = binomial)
10. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ comp + cleaned + (1 | block), family = binomial)
11. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ comp + cage + (1 | block), family = binomial)
12. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ cleaned + cage + (1 | block), family = binomial)
Three way combinations of treatments
13. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ light + comp + cage + (1 | block), family = binomial)
14. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ light + comp + cleaned + (1 | block), family = binomial)
15. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ light + cage + cleaned + (1 | block), family = binomial)
16. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ comp + cage + cleaned + (1 | block), family = binomial)
###All single factors together (no interactions)
17. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ light + comp + cage + cleaned + (1 | block), family = binomial)
All single factors plus interactions
18. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ light + comp + cage + cleaned + cage:cleaned + light:cleaned + light:cage + light:comp + (1 | block), family = binomial)
19. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ light + comp + cage + cleaned + light:cleaned + (1 | block), family = binomial)
20. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ light + comp + cage + cleaned + light:cage + (1 | block), family = binomial)
21. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ light + comp + cage + cleaned + light:comp + (1 | block), family = binomial)
22. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ light + comp + cage + cleaned + cage:cleaned + (1 | block), family = binomial)
Leaving out competition
23. lmer(cbind(cumul.germ.to.T7, (total.seeds.planted-cumul.germ.to.T7)) ~ light + cage + cleaned + comp:cleaned + (1 | block), family = binomial)

APPENDIX 5.1b List of all models used to test the effects of experimental treatments and their interactions on seedling height growth after 3.5 years.

Global model
1. lmer(mean.height ~ light + comp + cage + cleaned + (1 | block), family = gaussian, REML = FALSE)
Null
2. lmer(mean.height ~ + (1 | block), family = gaussian, REML = FALSE)
Light only
3. lmer(mean.height ~ light + (1 | block), family = gaussian, REML = FALSE)
Cage only
4. lmer(mean.height ~ cage + (1 | block), family = gaussian, REML = FALSE)
Competition only
5. lmer(mean.height ~ comp + (1 | block), family = gaussian, REML = FALSE)
Cleaned only
6. lmer(mean.height ~ cleaned + (1 | block), family = gaussian, REML = FALSE)
Light and light cage interaction
7. lmer(mean.height ~ light + light:cage + (1 | block), family = gaussian, REML = FALSE)

APPENDIX 5.2 Parameter estimates and standard errors

APPENDIX 5.2a Parameter estimates and standard errors for treatments and levels that appeared in top model for the binomial response percent germination after 1 year.

Species	Treatment	Level	Estimate	S.E
Coprosma propinqua	Intercept *(M 15)*		-2.49	0.31
	Light	Shade	1.62	0.19
	Fruit	Whole	-0.73	0.17
	Cage	Open	-0.76	0.17
Coprosma petriei	Intercept (*M 1*)		-2.92	0.44
	Light	Shade	1.77	0.40
	Fruit	Whole	-0.90	0.46
	Competition	Non-dug	-0.78	0.47
	Cage	Open	-0.36	0.45
	Light:Competition	Shade:Non-dug	-0.91	0.45
	Light:Cage	Shade:Open	-0.29	0.44
	Light:Fruit	Shade:Whole	0.27	0.43
	Competition:Cage	Non-dug:Open	1.55	0.39
	Competition:Fruit	Non-dug:Whole	0.98	0.39
	Cage:Cleaned	Open:Whole	-0.08	0.39
Aristotelia fruticosa	Intercept (*M 21*)		-3.00	0.46
	Light	Shade	1.43	0.34
	Fruit	Clean	-0.62	0.23
	Competition	Non-dug	-1.82	0.77
	Cage	Cage	-1.20	0.25
	Light:Competition	Shade:Non-dug	1.75	0.81

APPENDIX 5.2b Parameter estimates and standard errors for treatments and levels that appeared in the top model for the binomial response percent germination after 3.5 years.

Species	Treatment	Level	Estimate	S.E.
Coprosma propinqua	Intercept *(M 23)*		-1.38	0.19
	Light	Shade	0.95	0.13
	Cage	Open	-0.59	0.12
	Cleaned	Whole	-0.09	0.17
	Cleaned:Comp	Hand:Non-dug	0.17	0.17
	Cleaned:Comp	Whole:Non-dug	-0.41	0.18
Coprosma petriei	Intercept *(M 21)*		-2.81	0.31
	Light	Shade	1.79	0.25
	Comp	Non-dug	0.66	0.27
	Cage	Open	0.23	0.14
	Cleaned	Whole	-0.37	0.14
	Light:Comp	Shade:Non-dug	-0.95	0.32
Aristotelia fruticosa	Intercept *(M 8)*		-1.11	0.24
	Light	Shade	0.00	0.16
	Cleaned	Whole	-0.26	0.14
Corokia cotoneaster	Intercept *(M 18)*		-3.39	0.43
	Light	Shade	2.41	0.42
	Comp	Non-dug	0.92	0.39
	Cage	Open	0.05	0.37
	Cleaned	Whole	-1.06	0.43
	Cage:Cleaned	Open: Whole	0.24	0.35
	Light:Cleaned	Shade:Whole	0.79	0.43
	Light:Cage	Shade:Open	-1.04	0.41
	Light:Comp	Shade:Non-dug	-0.99	0.43
Leucopogon colensoi	Intercept *(M 13)*		-3.49	0.42
	Light	Shade	1.31	0.16
	Comp	Non-dug	0.40	0.14
	Cage	Open	-0.38	0.14
Leucopogon fraseri	Intercept *(M 20)*		-4.00	0.79
	Light	Shade	1.43	0.60
	Comp	Non-dug	-0.67	0.36
	Cage	Open	1.17	0.44
	Cleaned	Whole	-1.51	0.42
	Light:Cage	Shade:Open	-3.32	1.16
Gaultheria depressa	Intercept *(M 3)*		-8.03	0.57
	Light	Shade	0.73	0.35
Podocarpus nivalis	Intercept *(M 1)*		-5.31	1.30
	Light	Shade	-0.10	1.42
	Comp	Non-dug	-0.10	1.42
	Cage	Open	-0.10	1.42
	Cleaned	Whole	-35.48	7598.71

Light:Comp	Shade:Non-dug	1.40	1.80
Light:Cage	Shade:Open	1.76	1.78
Light:Cleaned	Shade:Whole	18.31	5332.19
Comp:Cage	Non-dug:Open	-2.96	1.64
Comp:Cleaned	Non-dug:Cleaned	-18.21	5084.73
Cage:Cleaned	Open: Whole	18.34	5413.70

APPENDIX 5.2c Parameter estimates and standard errors for treatments and levels that appeared in the top model for the binomial response percent seedling survival after 3.5 years.

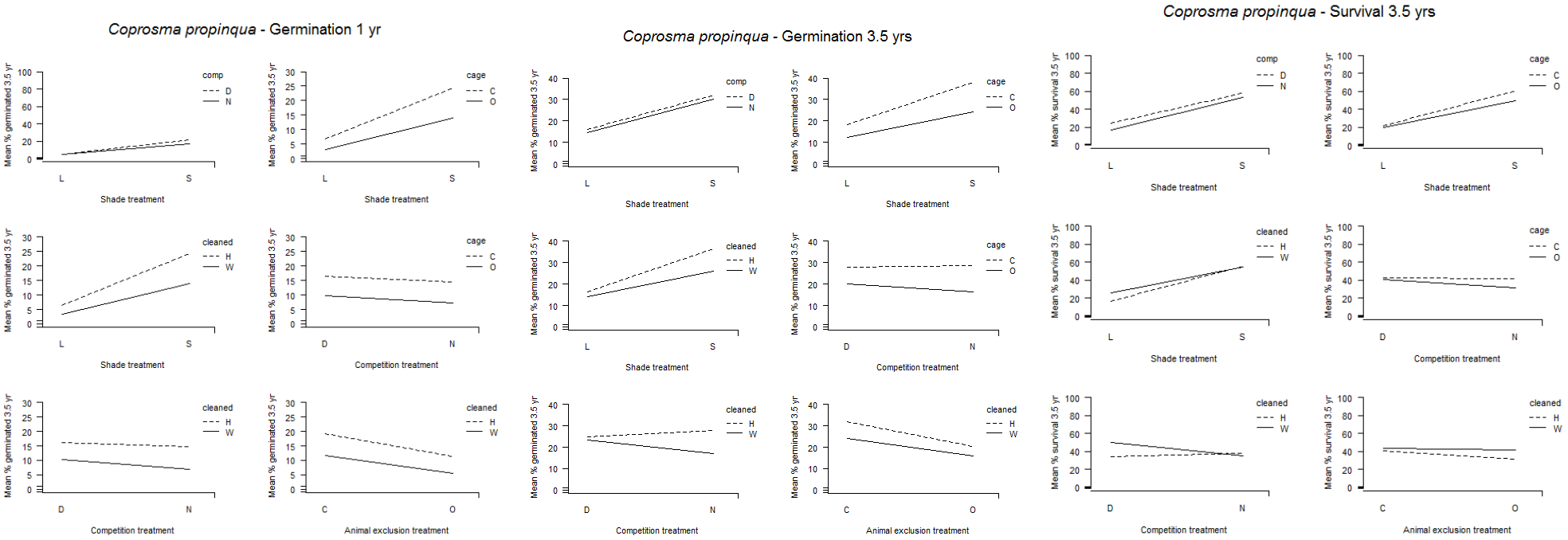
Species	Treatment	Level	Estimate	S.E.
Coprosma propinqua	Intercept *(M 3)*		-1.74	0.11
	Light	Shade	-0.73	0.16
Coprosma petriei	Intercept *(M 5)*		-1.97	0.11
	Cleaned	Whole	0.31	0.16
Aristotelia fruticosa	Intercept *(M 2)*		-1.83	0.13
Corokia cotoneaster	Intercept *(M 9)*		-5.48	1.11
	Light	Shade	-1.13	0.72
	Cage	Open	2.32	1.08
Leucopogon colensoi	Intercept *(M 13)*		-23.44	14175.79
	Light	Shade	19.67	14175.79
	Comp	Non-dug	-20.5	12256.15
	Cage	Cage	-20.01	13003.06
Gaultheria depressa	Intercept *(M 14)*		-2E+02	2E+07
	Light	Shade	-2E+01	6E+01
	Comp	Non-dug	7E+01	2E+07
	Cleaned	Whole	9E+01	2E+07

APPENDIX 5.2d Parameter estimates and standard errors for treatments and levels that appeared in the top model for the gaussian response seedling heights at 3.5 years.

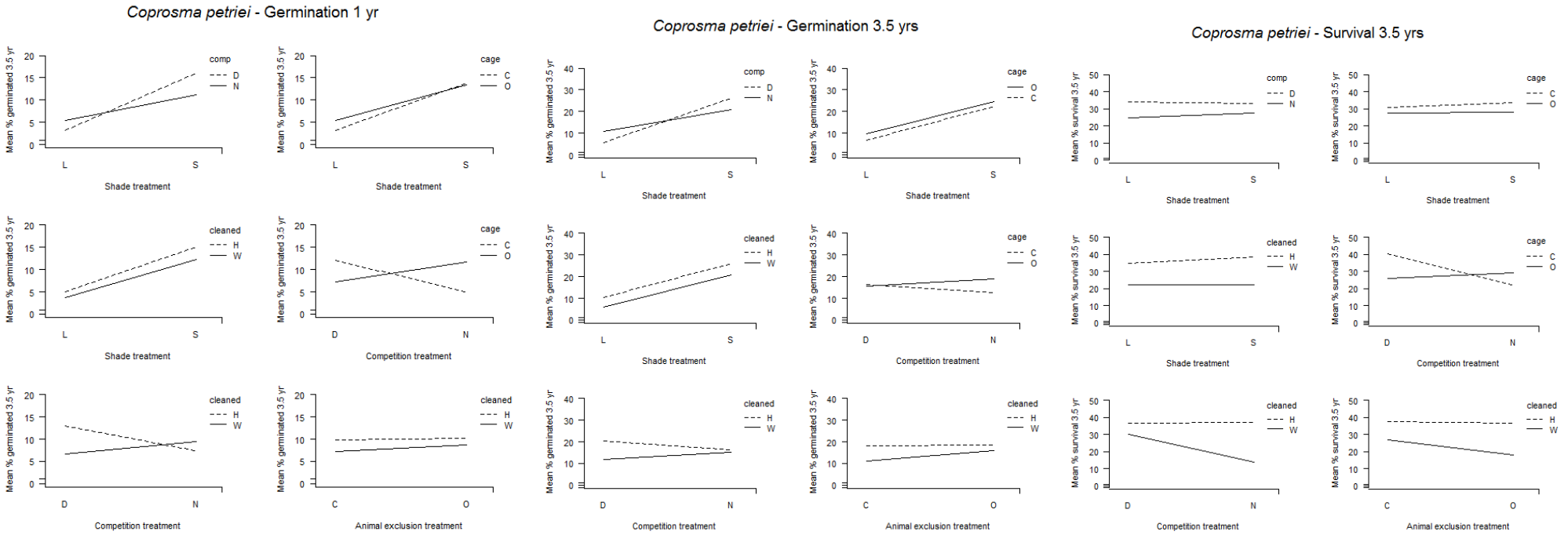
Species	Treatment	Level	Estimate	S.E.
Coprosma propinqua	Intercept *(M 3)*		2.24	0.28
	Light	Shade	1.19	0.26
Aristotelia fruticosa	Intercept *(M 3)*		1.24	0.39
	Light	Shade	4.61	0.71
Corokia cotoneaster	Intercept *(M 3)*		2.09	0.17
	Light	Shade	1.35	0.21

APPENDIX 5.3 Interaction plots for germination and seedling survival

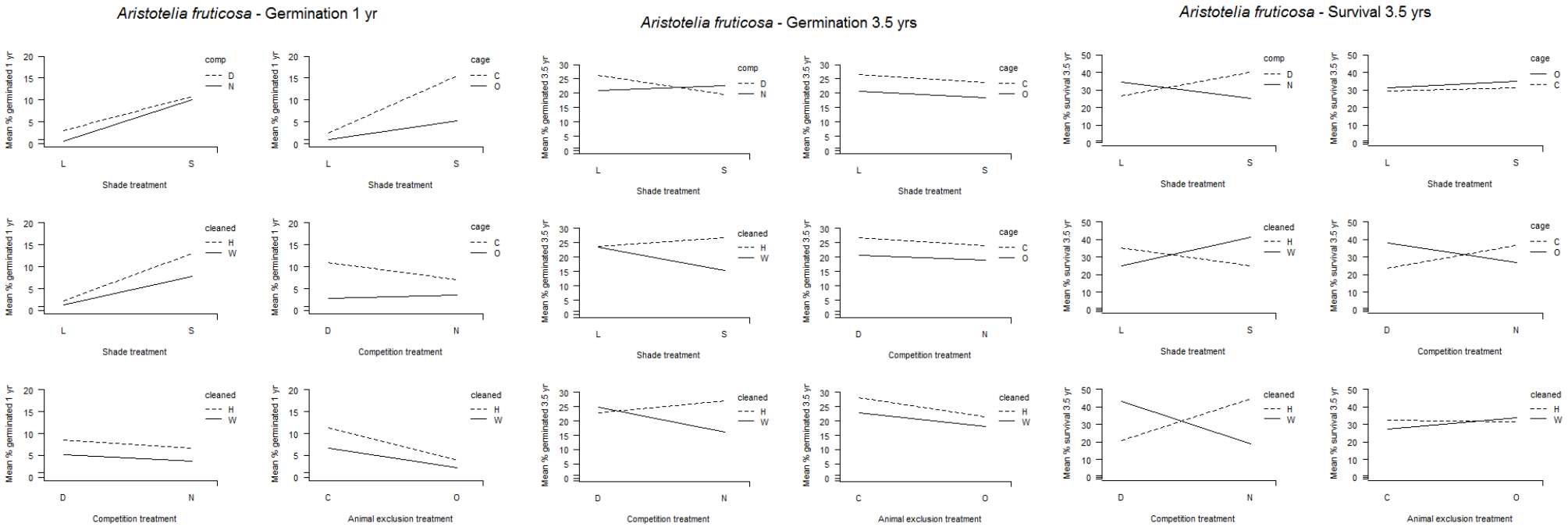
APPENDIX 5.3a – *Coprosma propinqua* interaction plots for germination success at 1 and 3.5 years, and seedling survival at 3.5 years.



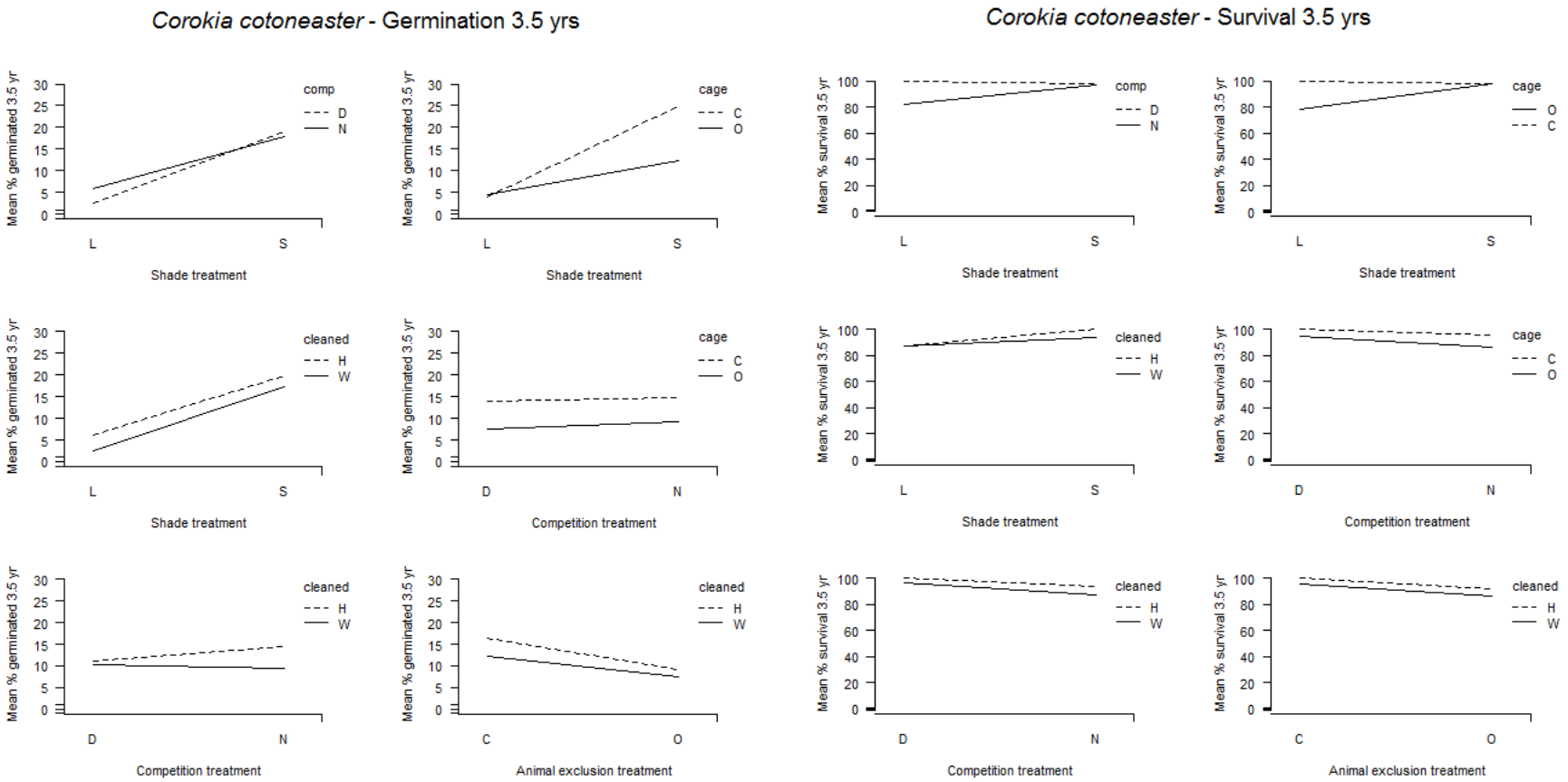
APPENDIX 5.3b – *Coprosma petriei* interaction plots for germination success at 1 and 3.5 years, and seedling survival at 3.5 years.



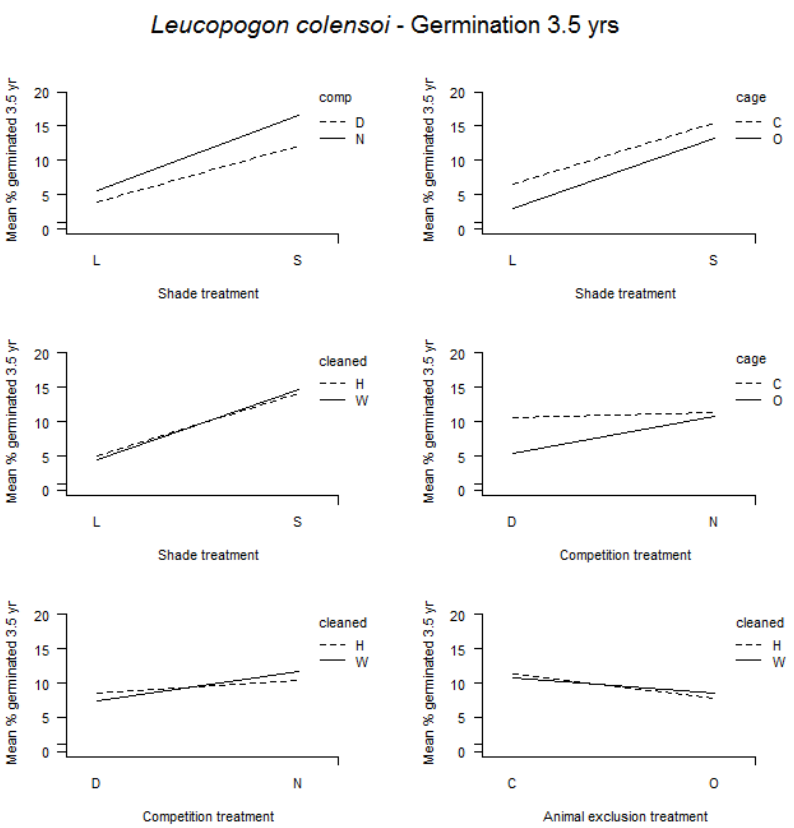
APPENDIX 5.3c– *Aristotelia fruticosa* interaction plots for germination success at 1 and 3.5 years, and seedling survival at 3.5 years.

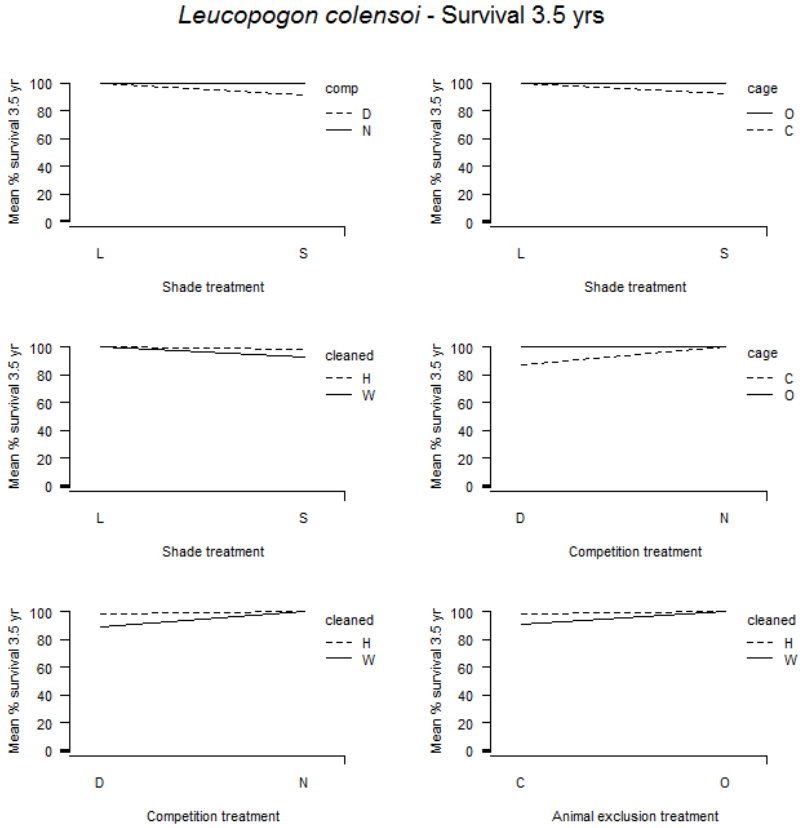


APPENDIX 5.3d – *Corokia cotoneaster* interaction plots for germination success at 3.5 years, and seedling survival at 3.5 years.

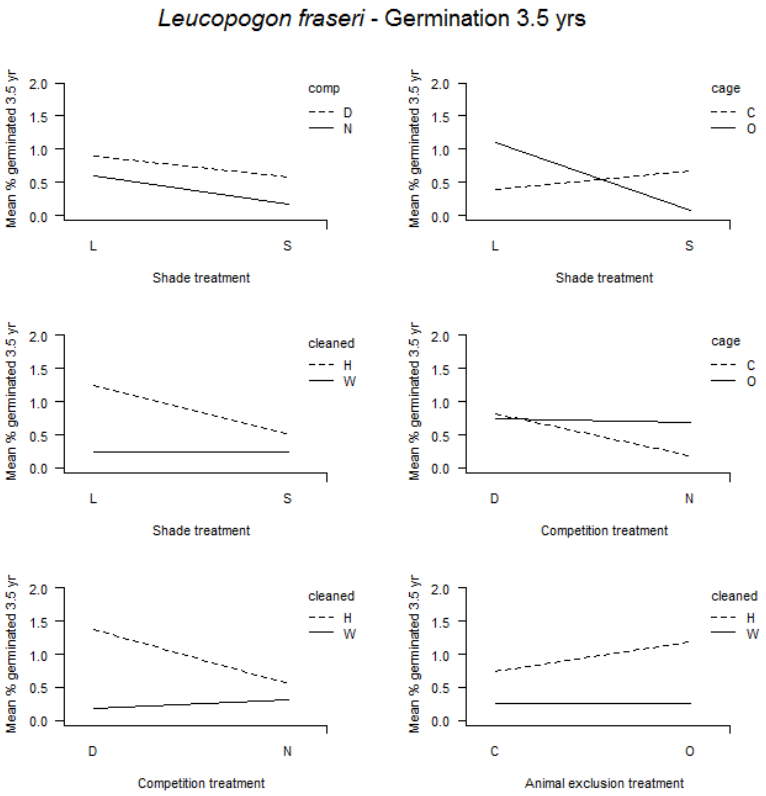


APPENDIX 5.3e – *Leucopogon colensoi* interaction plots for germination success at 3.5 years, and seedling survival at 3.5 years.

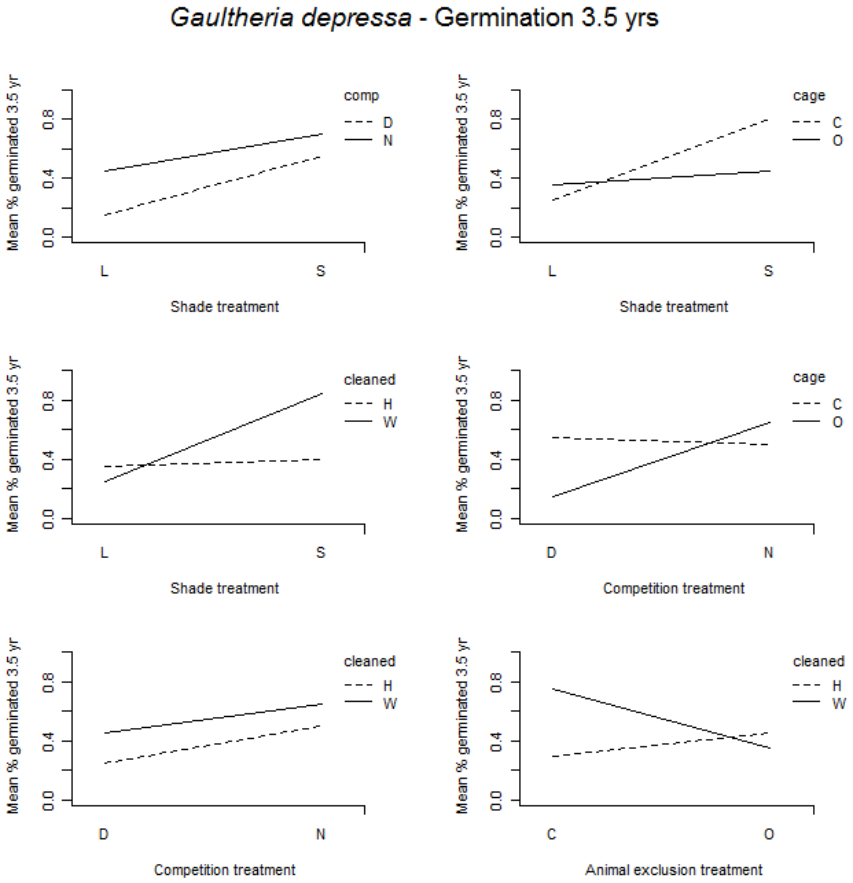




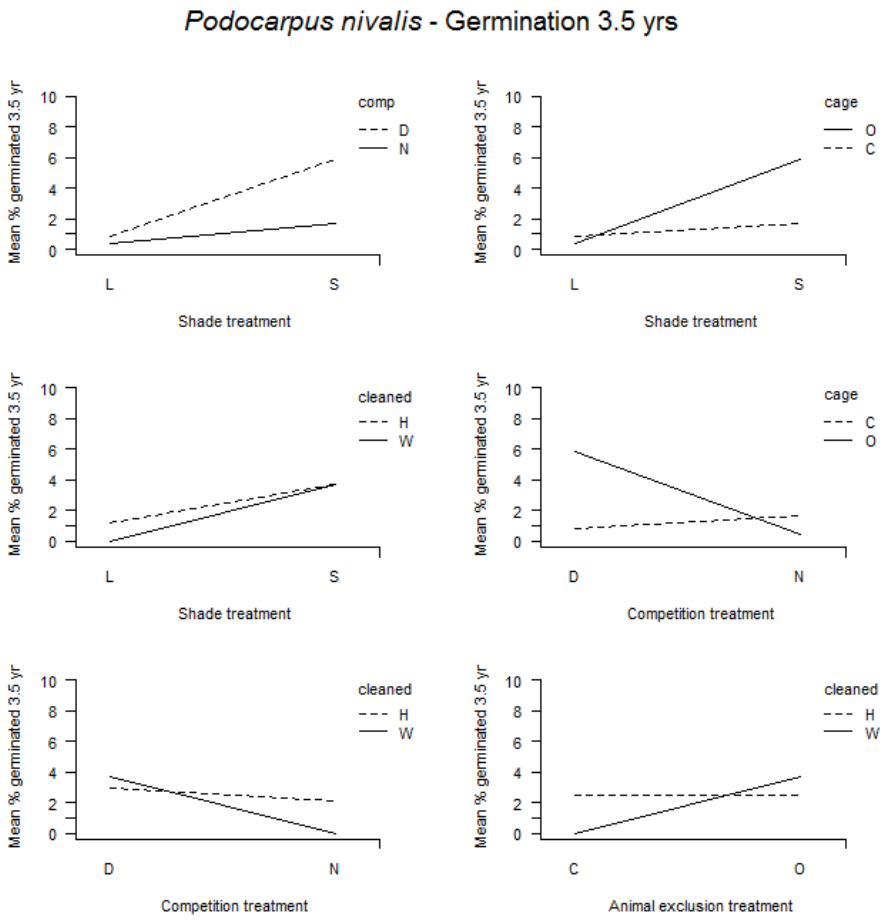
APPENDIX 5.3f – *Leucopogon fraseri* interaction plots for germination success at 3.5 years. Seedling survival at 3.5 years could not be plotted due to too few data points.



APPENDIX 5.3g – *Gaultheria depressa* interaction plots for germination success at 3.5 year and seedling survival at 3.5 years.



APPENDIX 5.3h – *Podocarpus nivalis* interaction plots for germination success at 3.5 year and seedling survival at 3.5 years.



CHAPTER SIX

Synthesis

Mixed association of prostrate fruiting alpine species, *Pentachondra pumila* (red) and *Leucopogon fraseri* (orange), both in the family Ericaceae.
(Photo: L.M. Young)

The main objective of this thesis was to assess whether seed dispersal mutualisms are functioning effectively in New Zealand montane and alpine ecosystems. This chapter synthesises the main findings from the thesis, puts the objectives in both a local and global perspective, and discusses future research directions and practical implications.

Until now, very little research on frugivore-mediated seed dispersal mutualisms in alpine ecosystems has been done in New Zealand or alpine systems elsewhere (but see Hulber, 2005; Muñoz and Cavieres, 2006). Relatively little was known about the dispersal effectiveness of introduced mammals (other than possums, Cowan, 1990; Williams et al., 2000; Dungan et al., 2002) for New Zealand native plants, and their net impact on plant recruitment. In the New Zealand setting, there have been no dispersal studies done at a community level, whereby all interactions between plants and the full suite of potential dispersers (native and exotic) have been evaluated. Most studies focus on the dispersal of a single plant or by a single animal species (e.g., Ladley and Kelly, 1996; Wotton, 2002; Kelly et al., 2004; Robertson et al., 2008; Larsen and Burns, 2012; O'Connor and Kelly, 2012) often omitting aspects of either dispersal quantity or quality. From a global perspective, most dispersal network studies use animal foraging observation (pre-dispersal) data to determine seed dispersal effectiveness (e.g., Schleuning et al., 2011), which may be less informative than studies which use faecal sampling, as we cannot accurately determine post-dispersal seed fates. Additionally, existing dispersal-mutualism networks are comprised largely of co-evolved interacting species, rather than dominated by novel species. However, the importance of novel species interactions is increasingly being acknowledged (Norton and Miller, 2000; Corlett, 2011).

Through following the various stages in the dispersal process (from fruit removal through to the relative effectiveness of dispersers and the (short-term) outcome for plants) for a range of species, this research has increased what we collectively know about dispersal mutualisms in New Zealand. In the mountains of Canterbury, I found that final percent fruit removal over two years in open-access treatments ranged from 25–60% among nine common montane and alpine plant species. Compared with other studies, the range in fruit removal levels found here was relatively low. For some species, fruits were slow to be removed while others remained on plants throughout winter. I showed that introduced mammals (especially possums, rabbits, hares, sheep, pigs and hedgehogs) were abundant and widespread through montane and alpine habitat and dispersed surprisingly large quantities of native fruits. Seeds from 67 plant species (mostly native) were

collectively dispersed by mammals and birds, and most animals excreted more than 90% of dispersed seeds intact. Possums were numerically the most important disperser, yet moved most seeds into mountain beech forest remnants. Rabbits, hares, and sheep were also numerically important, but dispersed seeds mainly into open grassland dominated by thick swards of exotic grasses. All are less suitable microsites than partial shade on the edge of shrubs. Kea are the largest and most mobile of only three remaining native alpine bird species, but are usually considered to be seed predators (because parrots typically feed directly on the seed embryo). However, I found that kea damage very few seeds, are numerically more important as seed dispersers than all other birds combined, and are probably responsible for most dispersal of seeds between mountain ranges. Finally, I investigated the effects of seed deposition microsite (shady/high-light), pulp-removal (whole/cleaned), competition (soil dug/not-dug) and predation (caged/not) on germination, growth and survival of eight montane and alpine plant species and related this to the spatial deposition of animal faeces. I found strong positive effects of shaded microsites for seed germination and seedling survival to 3.5 years for six of the eight species. Overall, both native birds and introduced mammals were dispersing alpine seeds, but mammals often deposited large numbers of seeds in habitats unsuitable for establishment.

This research aids in our general understanding of the importance of incorporating novel species assemblages in novel landscapes. Novel ecosystems have species compositions and relative abundances that have not occurred previously within a given biome (Odum, 1962), with the potential for changes in ecosystem functioning (Hobbs et al., 2006). In a recent review, Corlett (2011) highlighted that frugivory and seed dispersal mutualisms are at least as important in novel landscapes as in the natural landscapes that they replaced, but that they are likely to be less predictable in the absence of a shared evolutionary history. A more mechanistic understanding of all the processes of seed dispersal (e.g., gut-passage, germination microsite) is therefore needed to make robust predictions about what the outcomes of novel frugivore-plant interactions will be (Corlett, 2011). I show that each animal provides a unique contribution to seed dispersal effectiveness, and assessing dispersal mutualisms from a community perspective can provide a comprehensive mechanistic understanding about their relative effects on overall plant fitness.

What we have learned and future research

Kelly et al. (2010) recently published an extensive review evaluating the status of pollination and fruit dispersal in New Zealand. They offer an extensive framework, based on what we know, of future research directions and identify what we should focus on in future research. Below I use the five main conclusions identified by Kelly et al. (2010) to assess the contributions offered by this study in the wider context of what we know about seed dispersal effectiveness in New Zealand. I begin each of the five sections with the direct statement from Kelly et al. (2010) of what is needed in future research.

"First, we need more measurements of dispersal quantity on the mainland…" My data have nearly doubled the number of species that we know something about fruit removal for, and provided the first measurements from the relatively low animal-density alpine zone on the mainland.

"Second, there is a strong need for better quantitative measures of dispersal effectiveness, comparable to the Pollen Limitation Index for pollination failure…" Indeed we need better quantification of dispersal effectiveness in order to assess the overall effects on plant fitness, particularly when considering the impacts of exotic animal dispersers in a given system. Because there is no such index available, it was difficult to ascertain whether final levels of percent fruit removal (25-60%) were adequate (Chapter 2). Fruit removal only provides part of the picture, i.e. dispersal quantity, but fails to inform us about the final seed fate (Rodríguez-Pérez et al., 2012). Globally, functional roles of different types of frugivores are well documented for the fruit removal stage of dispersal, but not for the seed deposition stage (Jordano et al., 2007). Therefore it is necessary to incorporate as many qualitative aspects of dispersal as possible (e.g., gut-passage and seed treatment; microsite conditions) and how they affect long-term plant fitness (where possible), when creating a dispersal effectiveness index. My study has demonstrated the importance of each stage of dispersal for seedling recruitment (over 3.5 years) in relation to the actual spatial patterns of seed deposition, while considering the differential roles of most of the available dispersers. The probabilities of germination and survival decreased most strongly when a seed was dispersed into an unsuitable (high-light) microsite. Many exotic mammalian dispersers were moving seeds to these unfavourable microsites. These results therefore provide a mechanistic understanding of the dispersal processes which are important in determining plant fitness. If studies on fruit removal (Chapter 2) or faecal deposition/seed analysis (Chapter 3) were carried out alone, we would have little

understanding of how this contributed to overall plant fitness beyond the seed-movement stage. Alternatively, if studies focused solely on later stages of dispersal (as in Chapter 5), we would gain an understanding of factors that are important for germination and survival, but no realistic basis for its application. Therefore, by combining observational and experimental approaches from both the animal and the plant perspective, along multiple stages of the dispersal process, we can now use this kind of study as a framework to assess overall seed dispersal effectiveness.

"Third, we need to test the effect on regeneration if larger frugivores become rare or locally extinct, and only smaller frugivores are taking the smallest individual seeds…" This is of most concern for lower-altitude plant species in forest communities (see Wotton and Kelly, 2011). In montane and alpine systems, fruits and seeds are all small (< 5mm), and most frugivores larger than grasshoppers could ingest whole seeds. This brings attention to the potential importance of very small animals as alpine seed dispersal agents. Invertebrates (particularly Orthopterans), and lizards could then be important for local dispersal events if most seeds are excreted intact and moved to good quality microsites. Evidence for such dispersal events by alpine invertebrates has recently been shown for scree weta (Larsen and Burns, 2012) and grasshoppers (Young et al., 2012) for small-seeded *Gaultheria depressa* fruits. Overall, the fleshy-fruited alpine flora is perhaps more resilient than other floristic communities to the loss of larger dispersers because of its small fruit sizes.

"Fourth, we have little idea of how much longer-distance dispersal is necessary for the maintenance of meta-populations at the landscape scale." Seed dispersal is important for gene flow among fragmented populations (Hamilton, 1999; Garcia et al., 2007), particularly for isolated mountain tops separated by forested matrices. Modelling and molecular techniques are ideal ways to examine dispersal distances, seed shadows (Holbrook and Smith, 2000; Westcott et al., 2005; Russo et al., 2006; Wotton, 2007) and genotypic variation among fragments (Jordano et al., 2007), but these methods can sometimes be difficult and/or costly. Few birds are likely to make regular long-distance flights between isolated lowland forest remnants (except the New Zealand pigeon *Hemiphaga novaeseelandiae* (Wotton, 2007) and tui *Prosthemadera novaeseelandiae* (O'Connor, 2006) and even fewer regular long-distance fliers are evident in alpine areas (except kea *Nestor notabilis*). While kea populations are healthy in some areas of the South Island mountains, kea are absent from others, and non-existent in the North Island.

This leads to the obvious question of how alpine plants achieve long-distance dispersal events in the North Island (if at all). This question certainly warrants further investigation, as fossil evidence shows that kea were once present in the North Island (Holdaway and Worthy, 1993). North Island alpine areas are often smaller 'islands', generally more fragmented than the often continuous tracts of mountain chains along the Southern Alps, suggesting that long-distance dispersal events in those areas could be even more compromised than in the South Island due to the loss of kea for long-distance (between-mountain) dispersal events.

"Fifth, we need to find out whether introduced mammals are achieving some dispersal, and whether this is sufficient to maintain native plant meta-populations." A better understanding of the role of exotic species in ecosystem functioning (such as seed dispersal), has often been called for in the literature (Norton and Miller, 2000). Specialised dispersal mutualisms are not common because there are few benefits to the plant from being specialised, and it is difficult to exclude some dispersers from fruits (Wheelwright and Orians, 1982; Kelly et al., 2004). Thus dispersal mutualisms may overcome potential losses from the declining original disperser guild if fruits are able to be adequately removed from parent plants by replacement dispersers. In this study, there was indeed strong evidence for seed movement by replacement dispersers (i.e. exotic mammals). However, their relative overall effectiveness and fitness consequences for plants should always be considered in the light of any detrimental effects they may simultaneously have, (e.g., herbivory, browsing, trampling and competition with native biota). It is clear that most animals eat fruit at least occasionally, whether by chance or through targeted consumption, and thus it would be misleading to limit our focus only to native dispersal agents (unless the study has a co-evolutionary focus). Therefore, future studies of seed dispersal effectiveness and its consequences for plants should always incorporate the contribution by exotic disperser fauna.

We still need further investigation into the importance of large herbivorous ungulates and their potential for long distance dispersal events. I am currently working on the seed dispersal effectiveness by red deer (*Cervus elaphus*) by analysing faecal samples (collected during multiple fruiting seasons) from high-altitude sites around the South Island (results are intended for publication at a later date). In Europe, the United Kingdom, the Mediterranean, and Australia, for example, large roaming mammals such as deer are important seed dispersal agents (Welch, 1985; Davis et al., 2006, von Oheimb et al., 2005)

and unpublished data (L.M. Young) suggests they could also be important for some long-distance dispersal events in New Zealand.

High quality seed dispersal data can be obtained using fixed-area faecal sampling transects (or plots) and future work should consider using such sampling techniques. Although the faecal transect sampling methods used in Chapter 3 were not perfect, (in that they are inefficient at detecting faeces from the smallest mammals, birds and lizards), they were effective at measuring the relative abundance of faeces deposited in the landscape relative to body size, and consequently, the relative numerical contribution to seed dispersal by mammals at a landscape scale. Monitoring faecal transects over time is also beneficial because it incorporates spatial and temporal heterogeneities such as changes in the types of species dispersed with animal abundance, season and fruiting phenology. Additionally, using transects (or even search and detection methods) to collect faecal samples can provide a superior alternative to invasive techniques such as mist-netting of birds. Mist-netting birds purely for the purpose of investigating diet can subject birds to unnecessary stress and catch only a biased sub-sample of birds (Remsen and Good, 1996) and seeds.

Consequences of dispersal failure in warming alpine climates

Future climate change will have a major impact on biological diversity, especially in Arctic and alpine environments which will be exposed to the most extreme climatic changes (Thuiller et al., 2005; Mondoni et al., 2011). Many species adapted to these cold environments are expected to suffer range reduction following climate warming (Thuiller et al., 2005; Parmesan, 2006). Genetic variation is crucial for species to adapt to a changing climate and for long-term survival (Jump et al., 2009; Doi et al., 2010). Alsos et al. (2012) used empirical data to estimate loss of genetic diversity by loss of habitat for 27 plant species in the Arctic and the European Alps under existing climate scenarios. They found that species responded differently depending on a number of factors, including traits such as growth form and dispersal mode. Glacier crowfoot (*Ranunculus glacialis*) for example, grows only on mountain tops and has little gene flow between populations, and is thus expected to lose much of its genetic diversity in a warmer climate (Alsos et al., 2012). In general they found that species that utilize wind and birds to disperse their seeds will lose less of their genetic diversity in a warmer climate than species that have a very limited, or local, seed dispersal. This presumes that bird-dispersal is adequate between

populations.In many areas of New Zealand and elsewhere, there are few available dispersers, especially those capable of long-distance movements. If a species with limited seed dispersal is lost from an area, it means that the species as a whole will experience an irrevocable loss of genetic diversity (Alsos et al., 2012). Thus, knowledge of genetic diversity between fragmented populations for frugivore-dispersed (and also animal-pollinated) plants is needed to determine to what extent populations are under threat from climate change.

Practical implications

Restoring retired grazed or burnt high-country land

Knowledge of spatial patterning via frugivore-mediated dispersal of native plants could accelerate vegetation recovery in disturbed ecosystems. To date, the response of vegetation to disturbance in alpine habitats in New Zealand is poorly documented (Rogers and Leathwick, 1994; Lloyd et al., 2003). Increasingly, large areas of high country land are being retired from grazing or recovering from historic burns, and now 50% of the conservation estate in New Zealand (30% of the total land area) is on land above 500 m (Norton, 2000). How can these results assist with the restoration process in such areas of the New Zealand high country? At montane sites, open grassland provides relatively poor conditions for establishment of native seedlings. This could pose problems for management attempts to revert burnt native beech forest (often dominated by introduced grasses) through the successional pathway of shrubland, if seedlings cannot survive in direct competition with grasses. Rogers and Leathwick (1994) showed in one of the few related studies that exist in New Zealand montane or alpine communities, that steeper slopes had increased shrub establishment compared with gentler slopes in tussock grassland. They suggested that factors such as a reliably moist mineral substrate seemed important, but the ecological mechanisms require classification. Because we now understand some of the mechanisms driving seedling establisment and survival (in the short-term at least), we can provide guidelines to assist with the restoration process. The availability of perches on early-successional wind-dispersed shrubs within grasslands (e.g., *Leptospermum*, *Discaria*) could influence the behaviour of seed-dispersing birds, and consequently the establishment pattern of bird-dispersed plant species later in a successional sequence from grassland to shrubland (Rogers and Leathwick, 1994).

Management plans could consider assisting in the initial stages of the successional process by planting nursery-raised shrubs directly into the grasslands (of locally-eco-sourced seeds). This could encourage birds to those areas which would use them as a perch and defaecate seeds below the shrubs, depositing them into these microsites which we now know are more ideal for germination and survival of many plant species. Knowledge about how various native plants respond to safe microsites could speed up the restoration process and provide better chances of survival for subsequent naturally-dispersed seeds.

Overall, this research has shown the importance of evaluating multiple aspects of dispersal effectiveness, looking at native and exotic frugivores in novel ecosystems, and their relative contributions towards the long-term success for plant recruitment.

REFERENCES

Alsos, I.G., Ehrich, D., Thuiller, W., Eidesen, P.B., Tribsch, A., Schonswetter, P., Lagaye, C., Taberlet, P., Brochmann, C., 2012. Genetic consequences of climate change for northern plants. Proceedings of the Royal Society B: Biological Sciences.

Anderson, D.R., 2008. Model based inference in the life sciences: a primer on evidence. Springer.

Anderson, D.R., Burnham, K.P., Thompson, W.L., 2000. Null hypothesis testing: problems, prevalence and an alternative. Journal of Wildlife Management 64, 912-923.

Anderson, R., 1986. Keas for keeps, In Forest and Bird. pp. 2-5, New Zealand.

Anderson, S.H., Kelly, D., Ladley, J.J., Molloy, S., Terry, J., 2011. Cascading effects of bird functional extinction reduce pollination and plant density. Science 331, 1068-1071.

Anderson, S.H., Kelly, D., Robertson, A.W., Ladley, J.J., Innes, J.G., 2006. Birds as pollinators and dispersers: a case study from New Zealand. Acta Zoologica Sinica 52 (Supplement), 112-115.

Atkinson, I.A.E., Greenwood, R.M., 1989. Relationships between moas and plants. New Zealand Journal of Ecology 12, 67-96.

Atkinson, I.A.E., Millener, P.R., 1991. An ornithological glimpse into New Zealand's prehuman past., In Acta XX Congr Int Ornithol pp. 129-192

Bach, C.E., Kelly, D., 2007. Mistletoe fruit-colour polymorphism and differential success in a habitat mosaic. Austral Ecology 32, 509-514.

Ball, M.C., 1994. The role of photoinhibition during tree seedling establishment at low temperatures, In Photoinhibition of phototsynthesis: from molecular mechanisms to the field. eds N.R. Baker, J.R. Bowyer, pp. 365-376. BIOS Scientific Publishers, Oxford.

Bates, D., Maechler, M., Bolker, B., 2011. lme4: Linear Mixed-Effects Models Using S4 Classes., In R package version 0.999375-38, URL http://CRAN.R-project.org/package=lme4.

Battaglia, M., Reid, J.B., 1993. The effect of microsite variation on seed germination and seedling survival of *Eucalyptus delegatensis*. Australian Journal of Botany 41, 169-181.

Beavon, M., 2007 Pollination and dispersal of the noxious vine *Passiflora mollissima*. MSc in Environmental Science. University of Canterbury, Christchurch.

Bell, B., 1991. Recent avifauna changes and the history of ornithology in New Zealand. Acta XX Congressus Internationalis Ornithologici, 195-230.

Best, H.A., 1984. The foods of kakapo on Stewart Island as determined from their feeding sign. New Zealand Journal of Ecology 7, 71-83.

Beveridge, A.E., 1973. Regeneration of podocarps in central North Island forest. New Zealand Journal of Forestry 18, 23-35.

Blendinger, P.G., Villegas, M., 2011. Crop size is more important than neighborhood fruit availability for fruit removal of *Eugenia uniflora* (Myrtaceae) by bird seed dispersers. Plant Ecology and Diversity 212, 889-899.

Bliss, L.C., 1956. A comparison of plant development in microenvironments of Arctic and alpine tundras. Ecological Monographs 26, 303-337.

Boehning-Gaese, K., Gaese, B.H., Rabemanantsoa, S.B., 1999. Importance of primary and secondary seed dispersal in the Malagasy tree *Commiphora guillaumini*. Ecology 80, 821-832.

Bond, W.J., 1994. Do mutualisms matter - assessing the impact of pollinator and disperser disruption on plant extinction. Philosophical Transactions of the Royal Society of London Series B, Biology Sciences. 344, 83-90.

Boyes, R.S., Perrin, M.R., 2010. Patterns of daily activity of Meyers Parrot (*Poicephalus meyeri*) in the Okavango Delta, Botswana. Emu 110, 54-65.

Braun, J., 1913. Die vegetationsverhaltnisse der Schneestufe in den Rhatisch-Lepontinischen Alpen. Neue Denkschriften der Schweizerischen Naturforschenden Gesellschaft 48, 1-347.

Brejaart, R., 1988. Diet and feeding behaviour of the kea (*Nestor notabilis*). MSc Thesis, Lincoln College, New Zealand.

Bull, P.C., 1965. Birdlife. Nelson Lakes National Park Board, Nelson.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: A practical Information-Theoretic approach, 2nd edn. Springer-Verlag.

Burrows, C.J., 1977. Cass: history and science in the Cass District, Canterbury, New Zealand. University of Canterbury, Christchurch, New Zealand.

Burrows, C.J., 1981. The diet of moas based on gizzard contents samples from Pyramid Valley, North Canterbury, and Scaifes Lagoon, Lake Wanaka, Otago. Records of the Canterbury Museum 9, 309-336.

Burrows, C.J., 1989. Moa browsing: evidence from the Pyramid Valley mire. New Zealand Journal of Ecology 12, 51-56.

Burrows, C.J., 1994. Fruit types and seed dispersal modes of woody plants in Ahuriri Summit Bush, Port Hills, western Banks Peninsula, Canterbury, New Zealand. New Zealand Journal of Botany 32, 169-181.

Calviño-Cancela, M., 2002. Spatial patterns of seed dispersal and seedling recruitment in *Corema album* (Empetraceae): the importance of unspecialized dispersers for regeneration. Journal of Ecology 90, 775-784.

Campbell, B.A., 1976. Feeding habits of the kea in the Routeburn Basin. MSc Thesis, University of Otago, New Zealand.

Campos, C.M., Peco, B., Campos, V.E., Malo, J.E., Giannoni, S.M., Suarez, F., 2008. Endozoochory by native and exotic herbivores in dry areas: consequences for germination and survival of *Prosopis* seeds. Seed Science Research 18, 91-100.

Carlo, T.A., Collazo, J.A., Groom, M.J., 2003. Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. Oecologia 134, 119-131.

Carlo, T.A., Yang, S., 2011. Network models of frugivory and seed dispersal: Challenges and opportunities. Acta Oecologica 37, 619-624.

Chapman, C.A., Chapman, L.J., 1995. Plant-animal coevolution: is it thwarted by spatial and temporal variation in animal foraging?, In Seed dispersal and frugivory: ecology, evolution and conservation. eds D.J. Levey, W.R. Silva, M. Galetti. CAB International.

Christian, C.E., 2001. Consequences of a biological invasion reveal the importance of mutualism for plant communities. Nature 413, 635-639.

Clark, C.J., Poulsen, J.R., Bolker, B.M., Connor, E.F., Parker, V.T., 2005. Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. Ecology 86, 2684-2694.

Clarke, C.M.H., 1970. Observations of population, movement and food of the kea (*Nestor notabilis*). Notornis 17, 105-114.

Clout, M.N., Hay, J.R., 1989. The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. New Zealand Journal of Ecology 12, 27-33.

Coleman, J.D., Green, W., Q., Polson, J.G., 1985. Diet of brushtail possums over a pasture-alpine gradient in Westland, New Zealand. New Zealand Journal of Ecology 8, 21-35.

Collar, N.J., 1997. Family Psittacidae (Parrots), In Handbook of the Birds of the World. eds J. del Hoyo, A. Elliott, J. Sargatal. Lynx Edicions, Barcelona.

Connell, J.H., 1971. On the role of natural enemies in preventing competitive exclusion in some marine mammals and forest trees, In Dynamics of populations. eds P.J. den Boer, G.R. Gradwell, pp. 298-312. Centre for Agricultural Publishing and Documentation, Wageningen.

Cordeiro, N.J., Howe, H.F., 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. Proceedings of the National Academy of Sciences of the United States of America 100, 14052-14056.

Corlett, R.T., 1998. Frugivory and seed dispersal by vertebrates in the oriental (Indomalayan) region. Biological Reviews of the Cambridge Philosophical Society 73, 413-448.

Corlett, R.T., 2011. How to be a frugivore (in a changing world). Acta Oecologica 37, 674-681.

Cowan, P.E., 1990. Fruits, seeds and flowers in the diet of brushtail possums, *Trichosurus vulpecula*, in lowland podocarp/mixed hardwood forest, Orongorongo Valley, New Zealand. New Zealand Journal of Zoology 17, 549-566.

Cunningham, J.M., 1948. Number of keas. New Zealand Bird Notes 2, 154.

Diamond, J., Bond, A.B., 1999. Kea, bird of paradox. University of California Press, Berkley.

Diamond, J.M., 1984. Distribution of New Zealand birds on real and virtual islands. New Zealand Journal of Ecology 7, 37-55.

DOC, 2012. Department of Conservation Herpetofauna Database. Department of Conservation, New Zealand.

Doi, H.T., Takahashi, M., Katano, I., 2010 Genetic diversity increases regional variation in phenological dates in response to climate change. Global Change Biology 16, 373-379.

Dormann, C.F., Gruber, B., Frund, J., 2008. Introducing the bipartite Package: Analysing Ecological Networks. R news 8, 8-11.

Dudley, J.P., 2000. Seed dispersal by elephants in semiarid woodland habitats of Hwange National Park, Zimbabwe. Biotropica 32, 556-561.

Dungan, R.J., O'Cain, M.J., Lopez, M.L., Norton, D.A., 2002. Contribution by possums to seed rain and subsequent seed germination in successional vegetation, Canterbury, New Zealand. New Zealand Journal of Ecology 26, 121-128.

Duthie, C., Gibbs, G., Burns, K.C., 2006. Seed dispersal by weta. Science 311, 1575.

Elliott, G., Kemp, J., 2004. Effect of hunting and predation on kea, and a method of monitoring kea populations. Department of Conservation Internal Series 181, Wellington, New Zealand.

Fadzly, N., Burns, K.C., 2010. Hiding from the Ghost of Herbivory Past: Evidence for Crypsis in an Insular Tree Species. International Journal of Plant Sciences 171, 828-833.

Figuerola, J., Green, A.J., 2004. Effects of seed ingestion and herbivory by waterfowl on seedling establishment: A field experiment with wigeongrass *Ruppia maritima* in Doñana, South-West Spain. Plant Ecology 173, 33-38.

Fletcher, D., MacKenzie, D., Villouta, E., 2005 Modelling skewed data with many zeros: a simple approach combining ordinary and logistic regression. Environmental and Ecological Statistics 12, 45-54.

Forget, P.-M., Milleron, T., Feer, F., Henry, O., Dubost, G., 2000. Effects of dispersal pattern and mammalian herbivores on seedling recruitment for *Virola michelii* (Myristicaceae) in French Guiana. Biotropica 32, 452-462.

Forsyth, D.M., 2005. Chamois, In The Handbook of New Zealand Mammals. ed. C.M. King, pp. 351-361. Oxford University Press, Melbourne.

Forsyth, D.M., Coomes, D.A., Nugent, G., Hall, G.M.J., 2002. Diet and diet preferences of introduced ungulates (Order: Artiodactyla) in New Zealand. New Zealand Journal of Zoology 29, 323-344.

Forsyth, D.M., Tustin, K., 2005. Himalayan tahr, In The Handbook of New Zealand Mammals. ed. C.M. King, pp. 361-374. Oxford University Press, Melbourne.

Fowler, N.L., 1986. Microsite requirements for germination and establishment of three grass species. American Midland Naturalist 115, 131-145.

French, K., O'Dowd, D.J., Lill, A., 1992. Fruit removal of *Coprosma quadrifida* (Rubiaceae) by birds in south-eastern Australia. Australian Journal of Ecology 17, 35-42.

Gajdon, G.K., Fijn, N., Huber, L., 2004. Testing social learning in a wild mountain parrot, the kea (*Nestor notabilis*). Learning and Behavior 32, 62-71.

Galetti, M., 1993. Diet of the scaly-headed parrot (*Pionus maximiliani*) in a semideciduous forest in southeastern Brazil. Biotropica 25, 419-425.

Galetti, M., Donatti, C.I., Pizo, M.A., Giacomini, H.C., 2008. Big fish are the best: seed dispersal of *Bactris glaucescens* by the pacu fish (*Piaractus mesopotamicus*) in the Pantanal, Brazil. Biotropica 40, 386-389.

Galetti, M., Guimarães Jr., P.R., 2004. Seed dispersal of *Attalea phalerata* (Palmae) by crested caracaras (*Caracaras plancus*) in the Pantanal and a review of frugivory by raptors. Ararajuba 12, 133-135.

Galetti, M., Rodrigues, M., 1992. Comparative seed predation on pods by parrots in Brazil. Biotropica 24, 222-224.

García, C., Jordano, P., Godoy, J.A., 2007. Contemporary pollen and seed dispersal in a *Prunus mahaleb* population: patterns in distance and direction. Molecular Ecology 16, 1947-1955.

Garcia, D., Zamora, R., Amico, G.C., 2010. Birds as suppliers of seed dispersal in temperate ecosystems: conservation guidelines from real-world landscapes. Conservation Biology 24, 1070-1079.

Garrick, A.S., 1981. Diets of pipits and skylarks at Huirua Station, Tokomaru Bay, North Island, New Zealand. New Zealand Journal of Ecology 4, 106-114.

Gaston, K.J., Blackburn, T.M., Goldewijk, K.K., 2003. Habitat conversion and global avian biodiversity loss. Proceedings of the Royal Society of London B 270, 1293-1300.

Germino, M.J., Smith, W.K., 2000. High resistance to low-temperature photoinhibition in two alpine, snowbank species. Physiologia Plantarum 110, 89-95.

Glenny, D., Cruickshank, J., Rolfe, J., 2010. Key to Coprosma species of New Zealand http://www.landcareresearch.co.nz/research/biosystematics/plants/coprosmakey/. Landcare Research Manaaki Whenua, New Zealand.

Godinez-Alvarez, H., Valiente-Banuet, A., Rojas-MartInez, A., 2002. The role of seed dispersers in the population dynamics of the columnar cactus *Neobuxbaumia tetetzo*. Ecology 83, 2617-2629.

Gordon, D.P. ed., 2012. Kingdoms Bacteria, Protozoa, Chromista, Plantae, Fungi. Canterbury University Press.

Greenwood, R.M., Atkinson, I.A.E., 1977. Evolution of divaricating plants in New Zealand in relation to moa browsing. Proceedings of the New Zealand Ecological Society 24, 21-29.

Grubb, P.J., 1977. Maintenance of species richness in plant communities: importance of regeneration niche. Biological Reviews of the Cambridge Philosophical Society 52, 107-145.

Guimaraes Jr, P.R., Galetti, M., Jordano, P., 2008 Seed dispersal anachronisms: rethinking the fruits extinct megafauna ate PLoS ONE 3, e1745.

Halloy, S.R.P., Mark, A.F., 2003. Climate change effects on alpine plant biodiversity: A New Zealand perspective on quantifying the threat. Artic, Antarctic and Alpine Research 35, 248-254.

Hamilton, M.B., 1999. Tropical tree gene flow and seed dispersal. Nature 401, 129-130.

Hansen, D.M., Galetti, M., 2009. The Forgotten Megafauna. Science 324, 42-43.

Hansen, D.M., Kaiser, C.N., Müller, C.B., 2008. Endangered endemic plants on oceanic islands: seed dispersal, seedling establishment, and the use of ecological analogues. PLoS ONE 3, e2111.

Harper, J.L. ed., 1977. The population biology of plants. CAB International.

Harper, J.L., Clatworthy, J.N., McNaughton, I.H., Sagar, G.R., 1961. The evolution and ecology of closely related species living in the same area. Evolution 15, 209-227.

Harper, J.L., Williams, J.T., Sagar, G.R., 1965. The behaviour of seeds in soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. Journal of Ecology 53, 273-386.

Harper, P.L., Lovell, P.H., Moore, K.G., 1970. The shapes and sizes of seeds. Annual Review of Ecology and Systematics 1, 327-356.

Heather, B.D., Robertson, H.A., 1996. The Field Guide to the Birds of New Zealand. Viking, New Zealand.

Herrera, C.M., 2002. Seed dispersal by vertebrates, In Plant-animal interactions: an evolutionary approach. eds C.M. Herrera, O. Pellmyr, pp. 185-208. Blackwell Science.

Herrera, C.M., Jordano, P., 1981. *Prunus mahaleb* and birds: the high-efficiency seed dispersal system of a temperate fruiting tree. Ecological Monographs 51, 203-218.

Hitchmough, R.A., Bull, L., Cromarty, P., 2007. New Zealand Threat Classification Systems lists. Department of Conservation, Wellington, New Zealand.

Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography 15, 1-7.

Holbrook, K.M., Smith, T.B., Hardesty, B.D., 2002. Implications of long-distance movements of frugivorous rain forest hornbills. Ecography 25, 745-749.

Holdaway, R.N., Worthy, T.H., 1993. First North Island fossil record of kea, and morphological and morphometric comparison of kea and kaka. Notornis 40, 95-108.

Holdaway, R.N., 1989. New Zealand's pre-human avifauna and its vulnerability. New Zealand Journal of Ecology 12, 11-25.

Holdaway, R.N., Worthy, T.H., Tennyson, A.J.D., 2001. A working list of breeding bird species of the New Zealand region at first human contact. New Zealand Journal of Zoology 28, 119-187.

Horrocks, M., Costa, D., Wallace, R., Gardner, R., Kondo, R., 2004. Plant remains in coprolites: diet of a subalpine moa (Dinornithiformes) from southern New Zealand. Emu 104, 149-156.

Horrocks, M., Salter, J., Braggins, J., Nichol, S., Moorhouse, R., Elliott, G., 2008. Plant microfossil analysis of coprolites of the critically endangered kakapo (*Strigops habroptilus*) parrot from New Zealand. Review of Palaeobotany and Palynology 149, 229-245.

Howe, H.F., 1981. Dispersal of a neotropical nutmeg (*Virola sebifera*) by birds. Auk 98, 88-98.

Howe, H.F., 1989. Scatter- and clump-dispersal and seedling demography: hypothesis and implications. Oecologia 79, 417-426.

Howell, C.J., Kelly, D., Turnbull, M.H., 2002. Moa ghosts exorcised? New Zealand's divaricate shrubs avoid photoinhibition. Functional Ecology 16, 232-240.

Hülber, K., Ertl, S., Gottfried, M., Reiter, K., Grabherr, G., 2005. Gourmets or gourmands? Diet selection by large ungulates in high-alpine plant communities and possible impacts on plant propagation. Basic and Applied Ecology 6, 1-10.

Ingraham, N.L., Mark, A.F., 2000. Isotopic assessment of the hydrologic importance of fog deposition on tall snow tussock grass on southern New Zealand uplands. Austral Ecology 25, 402-408.

Innes, J., Kelly, D., Overton, J.M., Gillies, C., 2010. Predation and other factors currently limiting New Zealand forest birds. New Zealand Journal of Ecology 34, 86-114.

IUCN, 2011. Red List of Threatened Species, In Version 2011.2. .

Ivlev, V.S. ed., 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut, USA.

Izhaki, I., Safriel, U.N., 1990. The effect of some Mediterranean scrubland frugivores upon germination patterns. Journal of Ecology 78, 56-65.

Jackson, J.R., 1960. Keas at Arthurs Pass. Notornis 9, 39-58.

Janzen, D.H., 1970. Herbivores and number of tree species in tropical forests. American Naturalist 104, 501-508.

Janzen, D.H., 1981. *Ficus ovalis* seed predation by an orange-chinned parakeet (*Brotogeris jugularis*) in Costa-Rica. The Auk 98, 841-844.

Jerozolimski, A., Ribeiro, M.B.N., Martins, M., 2009. Are tortoises important seed dispersers in Amazonian forests? Oecologia 161, 517-528.

Jones, C., Sanders, M.D., 2005. European hedgehog, In The Handbook of New Zealand Mammals. ed. C.M. King, pp. 81-95. Oxford University Press, Melbourne.

Jordano, P., 1983. Fig-seed predation and dispersal by birds. Biotropica 15, 38-41.

Jordano, P., Garcia, C., Godoy, J.A., Garcia-Castano, J.L., 2007. Differential contribution of frugivores to complex seed dispersal patterns. Proceedings of the National Academy of Sciences of the United States of America 104, 3278-3282.

Jordano, P., Godoy, J.A., 2002. Frugivore-generated seed shadows: a landscape view of demographic and genetic effects, In Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. eds D.J. Levey, W.R. Silva, M. Galleti, pp. 305-321. CABI, Oxon.

Jordano, P., Schupp, E.W., 2000. Seed disperser effectiveness: The quantity component and patterns of seed rain for *Prunus mahaleb*. Ecological Monographs 70, 591-615.

Jump, A.S., Marchant, R., Peñuelas, J., 2009 Environmental change and the option value of genetic diversity. Trends in Plant Science 14, 51-58.

Kelly, D., Ladley, J.J., Robertson, A.W., 2004. Is dispersal easier than pollination? Two tests in New Zealand Loranthaceae. New Zealand Journal of Botany 42, 89-103.

Kelly, D., Robertson, A.W., Anderson, S.H., Ladley, J.J., Wotton, D.M., Wiser, S.K., 2010. Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit dispersal in New Zealand. New Zealand Journal of Ecology 34, 66-85.

King, C.M. ed., 2005. The Handbook of New Zealand Mammals, 2nd edn. Oxford University Press, Melbourne.

Krefting, L.W., Rowe, E., 1949. The role of some birds and mammals in seed germination. Ecological Monographs 19, 284-286.

Kudo, G., 1992. Performance and phenology of alpine herbs along a snow-melting gradient. Ecological Research 7, 297-304.

Ladley, J.J., Kelly, D., 1996. Dispersal, germination and survival of New Zealand mistletoes (Loranthaceae): Dependence on birds. . New Zealand Journal of Ecology 20, 69-79.

Larsen, H., Burns, K.C., In press. Seed dispersal effectiveness increases with body size in New Zealand alpine scree weta (*Deinacrida connectens*). Austral Ecology.

Lawrence, M.H., 1997. The importance of lizards to seed dispersal of native montane fleshy fruits, Canterbury, New Zealand. University of Canterbury, Christchurch.

Lee, W.G., Clout, M.N., Robertson, H.A., Wilson, J.B., 1991. Avian dispersers and fleshy fruits in New Zealand, In Acta XX Congressus Internationalis Ornithologici. ed. M.J. Williams, pp. 1617-1623, Wellington, New Zealand.

Lee, W.G., Weatherall, I.L., Wilson, J.B., 1994. Fruit conspicuousness in some New Zealand *Coprosma* (Rubiaceae) species. Oikos 69, 87-94.

Lee, W.G., Wilson, J.B., Johnson, P.N., 1988. Fruit colour in relation to the ecology and habit of *Coprosma* (Rubiaceae) species in New Zealand. Oikos 53, 325-331.

Lee, W.G., Wood, J.R., Rogers, G.M., 2010. Legacy of avian-dominated plant-herbivore systems in New Zealand. New Zealand Journal of Ecology 34, 28-47.

Lettink, M., Cree, A., Norbury, G., Seddon, P., 2008. Monitoring and restoration options for lizards on Kaitorete Spit, Canterbury, In Department of Conservation Research and Development Series. Department of Conservation, Wellington, New Zealand.

Levey, D.J., 1987. Seed size and fruit handling techniques of avian frugivores. American Naturalist 129, 471-485.

Levine, J.M., 2000. Species diversity and biological invasions: relating local process to community pattern. Science 288, 852-854.

Levine, J.M., Murrell, D.J., 2003. The community-level consequences of seed dispersal patterns. Annual Review of Ecology, Evolution, and Systematics 34, 549-574.

Liebst, B., Schneller, J., 2008. Seed dormancy and germination behaviour in two *Euphrasia* species (Orobanchaceae) occurring in the Swiss Alps. Botanical Journal of the Linnean Society 156, 649-656.

Lloyd, K.M., Lee, W.G., Fenner, M., Loughman, A.E., 2003. Vegetation change after artifical disturbance in an alpine *Chionochloa pallens* grassland in New Zealand. New Zealand Journal of Ecology 27, 31-36.

Loiselle, B.A., Blake, J.G., 1999. Dispersal of Melastome seeds by fruit-eating birds of tropical forest understory. Ecology 80, 330-336.

Lomascolo, S.B., Schaefer, H.M., 2010. Signal convergence in fruits: a result of selection by frugivores. Journal of Evolutionary Biology 23, 614-624.

López-Bao, J.V., González-Varo, J.P., 2011. Frugivory and spatial patterns of seed deposition by carnivorous mammals in anthropogenic landscapes: a multi-scale approach. PLoS ONE 6, e14569.

Lord, J., 1999. Fleshy-fruitedness in the New Zealand flora. Journal of Biogeography 26, 1249-1253.

Lord, J.M., 2004. Frugivore gape size and the evolution of fruit size and shape in southern hemisphere floras. Austral Ecology 29, 430-436.

Lord, J.M., Markey, A.S., Marshall, J., 2002. Have frugivores influenced the evolution of fruit traits in New Zealand, In Seed dispersal and frugivory: ecology, evolution and conservation. eds D.J. Levey, W.R. Silva, M. Galetti. CAB International.

Lord, J.M., Marshall, J., 2001. Correlations between growth form, habitat and fruit colour in the New Zealand flora, with special reference to frugivory by lizards. New Zealand Journal of Botany 39, 567-576.

Malo, J.E., Suárez, F., 1995. Herbivorous mammals as seed dispersers in a Mediterranean dehesa. Oecologia 104, 246-255.

Mark, A.F., Adams, N.M., 1995. New Zealand alpine plants, 2nd edn. Godwit Publishing, Auckland.

Mark, A.F., Dickinson, K.J.M., Hofstede, R.G.M., 2000. Alpine vegetation, plant distribution, life forms, and environments in a perhumid New Zealand region: oceanic and tropical high mountain affinities. Arctic, Antarctic, and Alpine Research 32, 240-254.

Marriner, G.R., 1908. The kea: a New Zealand problem, Christchurch.

Martínez, I., García, D., Obeso, J.R., 2008. Differential seed dispersal patterns generated by a common assemblage of vertebrate frugivores in three fleshy-fruited trees. Ecoscience 15, 189-199.

Mazerolle, M.J., 2009. AICcmodavg, Model selection and multimodel inference based on (Q)AIC(c), In R Package version 1.06.

McCarty, J.P., Levey, D.J., Greenberg, C.H., Sargent, S., 2002. Spatial and temporal variation in fruit use by wildlife in a forested landscape. Forest Ecology and Management 164, 277-291.

McConkey, K.R., Drake, D.R., 2002. Extinct pigeons and declining bat populations: are large seeds still being dispersed in the tropical Pacific? In Frugivory and seed dispersal: evolutionary and conservation perspectives. eds D. Levey, W. Silva, M. Galetti, pp. 381-395. CAB International, Wallingford, UK.

McGlone, M.S., Clarkson, B.D., 1993. Ghost stories: moa, plant defences and evolution in New Zealand. Tuatara 32.

McGlone, M.S., Webb, C.J., 1981. Selective forces influencing the evolution of divaricating plants. New Zealand Journal of Ecology 4, 20-28.

Michelsen-Heath, S., Gaze, P., 2007. Changes in abundance and distribution of the rock wren (*Xenicus gilviventrus*) in the South Island, New Zealand Notornis 54, 71-78.

Miskelly, C.M., Dowding, J.E., Elliott, G.P., Hitchmough, R.A., Powlesland, R.G., Robertson, H.A., Sagar, P.M., Scofield, R.P., Taylor, G.A., 2008. Conservation status of New Zealand birds. Notornis 55, 117-135.

Mondoni, A., Probert, R.J., Rossi, G., Vegini, E., Hay, F.R., 2011. Seeds of alpine plants are short lived: implications for long-term conservation. Annals of Botany 107, 171-179.

Muller-Landau, H.C., Wright, S.J., Calderón, O., Condit, R., Hubbell, S.P., 2008. Interspecific variation in primary seed dispersal in a tropical forest. Journal of Ecology, 96, 653-667.

Muñoz, A.A., Cavieres, L.A., 2006. A multi-species assessment of post-dispersal seed predation in the central Chilean Andes. Annals of Botany 98, 193-201.

Murphy, D.J., Kelly, D., 2001. Scarce or distracted? Bellbird (*Anthornis melanura*) foraging and diet in an area of inadequate mistletoe pollination. New Zealand Journal of Ecology 25, 69-81.

Murphy, S.R., Reid, N., Yan, Z.G., Venables, W.N., 1993. Differential passage time of mistletoe fruits through the gut of honeyeaters and flowerpeckers - effects on seedling establishment. Oecologia 93, 171-176.

Nathan, R., Muller-Landau, H.C., 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology and Evolution 15, 278-285.

Nogales, M., Hernandez, E.C., Valdes, F., 1999. Seed dispersal by common ravens *Corvus corax* among island habitats (Canarian Archipelago). Ecoscience 6, 56-61.

Norbury, G., Flux, J.E.C., 2005. Brown hare, In The Handbook of New Zealand Mammals. ed. C.M. King, pp. 151-159. Oxford University Press, Melbourne.

Norbury, G., Reddiex, B., 2005. European rabbit, In The Handbook of New Zealand Mammals. ed. C.M. King, pp. 131-151. Oxford University Press, Melbourne.

Norton, D., 2000. Conservation biology and private land: shifting the focus. Conservation Biology 14, 1221-1223.

Norton, D., Miller, C.J., 2000. Some issues and options for the conservation of native biodiversity in rural New Zealand. Ecological Management and Restoration 1, 26-34.

Nugent, G., Fraser, K.W., 2005. Red deer, In The handbook of New Zealand mammals. ed. C.M. King, pp. 410-420. Oxford University Press, Melbourne.

Nugent, G., Fraser, W., Sweetapple, P., 2001. Top down or bottom up? Comparing the impacts of introduced arboreal possums and 'terrestrial' ruminants on native forests in New Zealand. Biological Conservation 99, 65-79.

Nugent, G., Sweetapple, P.J., Coleman, J., Suisted, P. eds., 2000. Possum feeding patterns: dietary tactics of a reluctant folivore. Manaaki Whenua Press, Lincoln, New Zealand.

Nunez, M., Bowman, D.M.J.S., 1986. Nocturnal cooling in a high altitude stand of *Eucalyptus delegatensis* as related to stand density. Australian Forest Research 16, 185-197.

O'Connor, S-J., 2006. Modelling seed dispersal by tui, In School of Biological Sciences. University of Canterbury, Christchurch.

O'Connor, S-J., Kelly, D., In press. Seed dispersal of matai (*Prumnopitys taxifolia*) by feral pigs, *Sus scrofa*. New Zealand Journal of Ecology.

O'Donnell, C.F.J., Dilks, P.J., 1994. Foods and foraging of forest birds in temperate rainforest, South Westland, New Zealand. New Zealand Journal of Ecology 18, 87-107.

O'Dowd, D.J., Hay, M.E., 1980. Multalism between harvester ants and a desert ephemeral: seed escape from rodents. Ecology 61, 531-540.

Odum, H.T., 1962. Ecological tools and their use. man and the ecosystem, In Proceeding of the Lockwood conference on the suburban forest and ecology. eds P.E. Waggoner, J.D. Ovington, pp. 57-75. The Connecticut Agricultural Experiment Station Bulletin.

Olesen, J.M., Valido, A., 2003. Lizards as pollinators and seed dispersers: an island phenomenon. Trends in Ecology and Evolution 18, 177-181.

Osmond, C.B., 1981. Photorespiration and photoinhibition. Biochimica et biophysica acta (BR): Reviews on bioenergetics 639, 77-98.

Osmond, C.B., 1994. What is photoinhibition? Some insights from comparisons of shade and sun plants, In Photoinhibition of phototsynthesis: from molecular mechanisms to the field. eds N.R. Baker, J.R. Bowyer, pp. 433-447. BIOS Scientific Publishers, Oxford.

Padilla, D.P., Nogales, M., 2009. Behavior of kestrels feeding on frugivorous lizards: implications for secondary seed dispersal. Behavioural Ecology 20, 872-875.

Parkes, J.P., Thomson, C., 1995. Management of thar. Part II: diet of thar, chamois, and possums. Science for Conservation 7, 22-42.

Parmesan, C., 2006 Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution and Systematics 37, 637-669.

Peinetti, R., Pereyra, M., Kin, A., Sosa, A., 1993. Effects of cattle ingestion on viability and germination rate of calden (*Prosopis caldenia*) seeds. Journal of Range Management 46, 483-486.

Peres, C.A., Palacios, E., 2007. Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal-mediated seed dispersal. Biotropica 39, 304-315.

Primack, R.B., Miao, S.L., 1992. Dispersal can limit local plant distribution. Conservation Biology 6, 513-519.

Puckey, H.L., Lill, A., O'Dowd, D., 1996. Fruit color choices of captive silvereyes (*Zosterops lateralis*). Condor 98, 780-790.

Pullar, T., 1996. Kea (*Nestor notabilis*) captive management plan and husbandry manual. Department of Conservation Threatened Species Occasional Publication 9, Wellington, New Zealand.

R, 2011. R: A language and environment for statistical computing., In R Development Core Team. R Foundation for Statistical Computing, Vienna, Austria.

Ramos, M.E., Robles, A.B., Castro, J., 2006. The efficiency of endozoochorous seed dispersal in six dry-fruited species (Cistaceae) from seed ingestion to early seed establishment. Plant Ecology 185, 97-106.

Remsen, J.V., Good, D.A., 1996. Misuse of data from mist-net captures to assess relative abundance in bird populations. The Auk 113, 381-398.

Ridley, H.N. ed., 1930. The dispersal of plants throughout the world. Reeve, Ashford, Kent.

Robertson, A., Ladley, J.J., Kelly, D., McNutt, K.L., Peterson, P.P., Merrett, M.F., Karl, B.J., 2008. Assessing pollination and fruit dispersal in *Fuchsia excorticata* (Onagraceae). New Zealand Journal of Botany 46, 299-314.

Robertson, A.W., Trass, A., Ladley, J.J., Kelly, D., 2006. Assessing the benefits of frugivory for seed germination: the importance of the deinhibition effect. Functional Ecology 20, 58-66.

Rodríguez-Pérez, J., Wiegand, T., Santamaria, L., 2012. Frugivore behaviour determines plant distribution: a spatially-explicit analysis of a plant-disperser interaction. Ecography 35, 113-123.

Rogers, G.M., Leathwick, J.R., 1994. North Island seral tussock grasslands: 2. Autogenic succession: Change of tussock grassland to shrubland. New Zealand Journal of Botany 32, 287-303.

Rogers, G.M., Walker, S., Tubbs, M., Henderson, J., 2002. Ecology and conservation status of three "spring annual" herbs in dryland ecosystems of New Zealand. New Zealand Journal of Botany 40, 649-669.

Rose, A.B., Platt, K.H., Frampton, C.M., 1995. Vegetation change over 25 years in a New Zealand short-tussock grassland: effects of sheep grazing and adventive invasions. New Zealand Journal of Ecology 19, 163-174.

Russo, S.E., 2005. Linking seed fate to natural dispersal patterns: factors affecting predation and scatter-hoarding of *Virola calophylla* seeds in Peru. Journal of Tropical Ecology 21, 243-253.

Russo, S.E., Portnoy, S., Augspurger, C.K., 2006. Incorporating animal behavior into seed dispersal models: Implications for seed shadows. Ecology 87, 3160-3174.

Samuels, I.A., Levey, D.J., 2005. Effects of gut passage on seed germination: do experiments answer the questions they ask? Functional Ecology 19, 365-368.

Sazima, I., 2008. The parakeet *Brotogeris tirica* feeds on and disperses the fruits of the palm *Sygarus romanzoffiana* in Southeastern Brazil. Bioneotropica 8, 231-234.

Schleuning, M., Blüthgen, N., Flörchinger, M., Braun, J., Schaefer, H.M., Böhning-Gaese, K., 2010. Specialization and interaction strength in a tropical plant-frugivore network differ among forest strata. Ecology 92, 26-36.

Schupp, E.W., 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 108, 15-29.

Schupp, E.W., Fuentes, M., 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. Ecoscience 2, 267-275.

Schupp, E.W., Jordano, P., Gómez, J.M., 2010. Seed dispersal effectiveness revisited: a conceptual review. New Phytologist 188, 333-353.

Schwienbacher, E., Navarro-Cano, J.A., Neuner, G., Erschbamer, B., 2011. Seed dormancy in alpine species. Flora - Morphology, Distribution, Functional Ecology of Plants 206, 845-856.

Şekercioğlu, Ç.H., Daily, G.C., Ehrlich, P.R., 2004. Ecosystem consequences of bird declines. Proceedings of the National Academy of Sciences of the United States of America 101, 18042-18047.

Sessions, L., Kelly, D., 2000. The effects of browntop (*Agrostis capillaris*) dominance after fire on native shrub germination and survival. New Zealand Natural Sciences 25, 1-9.

Shanks, A., Glenny, D., Gibson, R., Rosser, K., Roozen, D., Phillipson, S., Steven, J., Arand, J., 1990. Coleridge, Craigieburn and Cass Ecological Districts. Survey Report for the Protected Natural Areas Programme. Department of Conservation, Wellington, New Zealand.

Sharam, G.J., Sinclair, A.R.E., Turkington, R., 2009. Serengeti birds maintain forests by inhibiting seed predators. Science 325, 51-51.

Silvertown, J., Tremlett, M., 1989. Interactive effects of disturbance and shade upon colonization of grassland: an experiment with *Anthriscus sylvestris*, *Conium maculatum*, *Daucus carota* and *Heracleum sphodylium*. Functional Ecology 3, 229-235.

Spiegel, O., Nathan, R., 2007. Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. Ecology Letters 10, 718-728.

Staddon, S.C., Compton, S.G., Portch, A., 2010. Dispersal of fig seeds in the Cook Islands: introduced frugivores are no substitute for natives. Biodiversity and Conservation 19, 1905-1916.

Svenning, J.C., 2001. On the role of microenvironmental heterogeneity in the ecology and diversification of neotropical rain-forest palms (Arecaceae). Botanical Review 67, 1-53.

Temple, P., 1996. The Book of the Kea. Hodder Moa Beckett Publishers Ltd, Auckland, New Zealand.

Tennyson, A.J.D., 2010. The origin and history of New Zealand's terrestrial vertebrates. New Zealand Journal of Ecology 34, 6-27.

Thorsen, M., Seddon, P., Dickinson, K., 2011. Faunal influences on New Zealand seed dispersal characteristics. Evolutionary Ecology 25, 1397-1426.

Thorsen, M.J., Dickinson, K.J.M., Seddon, P.J., 2009. Seed dispersal systems in the New Zealand flora. Perspectives in Plant Ecology, Evolution and Systematics 11, 285-309.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. Proceedings of the National Academy of Sciences of the United States of America 102, 8245-8250.

Tilman, D., 1985. The resource-ratio hypothesis of plant succession. The American Naturalist 125, 827-852.

Towns, D.R., Daugherty, C.H., 1994. Patterns of range contractions and extinctions in the New Zealand herpetofauna following human colonization. New Zealand Journal of Zoology 21, 325-339.

Trakhtenbrot, A., Nathan, R., Perry, G., Richardson, D.M., 2005. The importance of long-distance dispersal in biodiversity conservation. Diversity and Distributions 11, 173-181.

Traveset, A., 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. Perspectives in Plant Ecology, Evolution and Systematics 1, 151-190.

Traveset, A., Richardson, D.M., 2006. Biological invasions as disruptors of plant reproductive mutualisms. Trends in Ecology and Evolution 21, 208-216.

Traveset, A., Riera, N., 2005. Disruption of a plant-lizard seed dispersal system and its ecological effects on a threatened endemic plant in the Balearic Islands. Conservation Biology 19, 421-431.

Traveset, A., Riera, N., Mas, R.E., 2001. Passage through bird guts causes interspecific differences in seed germination characteristics. Functional Ecology 15, 669-675.

Traveset, A., Willson, M., 1998. Ecology of the fruit-colour polymorphism in *Rubus spectabilis*. Evolutionary Ecology 12, 331-345.

Urbanska, K.M., Schutz, M., 1986. Reproduction by seed in alpine plants and revegetation research above timberline. Botanica Helvetica 96, 43-60.

Valenta, K., Fedigan, L.M., 2009. Effect of gut passage, faeces and seed handling on latency and rate of germination in seeds consumed by capuchins (*Cebus capucinus*). American Journal of Physical Anthropology 138, 486-492.

van der Pijl, L. ed., 1972. Principles of dispersal in higher plants. Springer-Verlag, Würzburg.

van der Pijl, L., 1982. Principles of dispersal in higher plants, 2nd edn. Springer Verlag, Berlin.

Venn, S.E., Morgan, J.W., 2010. Soil seedbank composition and dynamics across alpine summits in south-eastern Australia. Australian Journal of Botany 58, 349-362.

von Oheimb, G., Schmidt, M., Kriebitzsch, W.-U., Ellenberg, H., 2005. Dispersal of vascular plants by game in northern Germany. Part II: Red deer (*Cervus elaphus*). European Journal of Forest Research 124, 55-65.

Wardle, P., 1964. Facets of the distribution of forest vegetation in New Zealand. The New Zealand Journal of Botany 2, 352-366.

Wardle, P., 1991. Vegetation of New Zealand, 2nd edn. Cambridge University Press.

Webb, C.J., Simpson, M.J.A. eds., 2001. Seeds of New Zealand: gymnosperms and dicotyledons. Manuka Press.

Welch, D., 1985. Studies in the grazing of heather moorland in north-east Scotland. Journal of Applied Ecology 22, 461-472.

Wenny, D.G., 2000. Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. Ecological Monographs 70, 331-351.

Wenny, D.G., DeVault, T.L., Johnson, M.D., Kelly, D., Sekercioglu, C.H., Tomback, D.F., Whelan, C.J., 2011. The need to quantify ecosystem services provided by birds. The Auk 128, 1-14.

Wenny, D.G., Levey, D.J., 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. Proceedings of the National Academy of Sciences 95, 6204-6207.

Westcott, D.A., Bentrupperbaumer, J., Bradford, M.G., McKeown, A., 2005. Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. Oecologia 146, 57-67.

Wheelwright, N.T., Orians, G.H., 1982. Seed dispersal by animals - contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. American Naturalist 119, 402-413.

Whitney, K.D., 2005. Evidence for simple genetic control of a fruit-colour polymorphism in *Acacia ligulata*. Australian Journal of Botany 53, 363-366.

Whitney, K.D., Stanton, M.L., 2004. Insect seed predators as novel agents of selection on fruit colour. Ecology 85, 2153-2160.

Whittaker, A.H., 1987. The roles of lizards in New Zealand plant reproductive strategies. New Zealand Journal of Botany 25, 315-328.

Willems, J.H., Huijsmans, K.G.A., 1994. Vertical seed dispersal by earthworms: a quantitative approach. Ecography 17, 124-130.

Williams, C.K., 1982. Nutritional properties of some fruits eaten by the possum *Trichosurus vulpecula* in a New Zealand broadleaf-podocarp forest. New Zealand Journal of Ecology 5, 16-20.

Williams, P.A., 2003. Are possums important dispersers of large-seeded fruit? New Zealand Journal of Ecology 27, 221-223.

Williams, P.A., Karl, B.J., 1996. Fleshy fruits of indigenous and adventive plants in the diet of birds in forest remnants, Nelson, New Zealand. New Zealand Journal of Ecology 20, 127-145.

Williams, P.A., Karl, B.J., Bannister, P., Lee, W.G., 2000. Small mammals as potential seed dispersers in New Zealand. Austral Ecology 25, 523-532.

Willson, M., 1994. Fruit choices by captive American robins. Condor 96, 494-502.

Willson, M., O'Dowd, D., 1989. Fruit color polymorphisms in a bird-dispersed shrub (*Rhagodia parabolica*) in Australia. Evolutionary Ecology 3, 40-50.

Willson, M.F., Irvine, A.K., Walsh, N.G., 1989. Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. Biotropica 21, 133-147.

Willson, M.F., Traveset, A., 2000. The ecology of seed dispersal, 2nd edn. CAB International

Willson, M.F., Whelan, C.J., 1990. The evolution of fruit color in fleshy-fruited plants. The American Naturalist 136, 790-809.

Wilmshurst, J.M., Anderson, A.J., Higham, T.F.G., Worthy, T.H., 2008. Dating the late prehistoric dispersal of polynesians to New Zealand using the commensal Pacific rat. Proceedings of the National Academy of Sciences of the United States of America 105, 7676-7680.

Wilson, D.J., Lee, W.G., Webster, R.A., Allen, R.B., 2003. Effects of possums and rats on seedling establishment at two forest sites in New Zealand. New Zealand Journal of Ecology 27, 147-155.

Wilson, H.D., 1994. Regeneration of native forest on Hinewai Reserve, Banks Peninsula. New Zealand Journal of Botany 32, 373-383.

Wilson, H.D., Galloway, T., 1993. Small-leaved shrubs of New Zealand. Manuka Press, Christchurch, New Zealand.

Wilton, A.D., Breitwieser, I., 2000. Composition of the New Zealand seed plant flora. New Zealand Journal of Botany 38, 357-549.

Wiser, S.K., Allen, R.B., Platt, K.H., 1997. Mountain beech forest succession after a fire at Mt. Thomas Forest, Canterbury, New Zealand. New Zealand Journal of Botany 35.

Wood, J.R., Rawlence, N.J., Rogers, G.M., Austin, J.J., Worthy, T.H., Cooper, A., 2008. Coprolite deposits reveal the diet and ecology of the extinct New Zealand megaherbivore moa (Aves, Dinornithiformes). Quaternary Science Reviews 27, 2593-2602.

Wotton, D.M., 2002. Effectiveness of the common gecko (*Hoplodactylus maculatus*) as a seed disperser on Mana Island, New Zealand. New Zealand Journal of Botany 40, 639-647.

Wotton, D.M., 2007. Consequences of dispersal failure: kereru and large seeds in New Zealand, PhD in School of Biological Sciences. University of Canterbury, Christchurch.

Wotton, D.M., Kelly, D., 2011. Frugivore loss limits recruitment of large-seeded trees. Proceedings of the Royal Society B: Biological Sciences.

Wright, S.J., Zeballos, H., Dominguez, I., Gallardo, M.M., Moreno, M.C., Ibanez, R., 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. Conservation Biology 14, 227-239.

Wyman, T.E., Trewick, S.A., Morgan-Richards, M., Noble, A.D.L., 2011. Mutualism or opportunism? Tree fuchsia (*Fuchsia excorticata*) and tree weta (*Hemideina*) interactions. Austral Ecology 36, 261-268.

Young, L.M., Bell, R.J.H., 2010. Frugivory and primary seed dispersal by a New Zealand falcon (*Falco novaeseelandiae*) at Red Tarns, Mt Sebastapol, New Zealand. Notornis 57, 94-95.

Young, L.M., Kelly, D., Nelson, X.J., 2012. Alpine flora may depend on declining frugivorous parrot for seed dispersal. Biological Conservation 147, 133-142.

Zedrosser, A., Steyaert, S.M.J.G., Gossow, H., Swenson, J.E., 2011. Brown bear conservation and the ghost of persecution past. Biological Conservation 144, 2163-2170.

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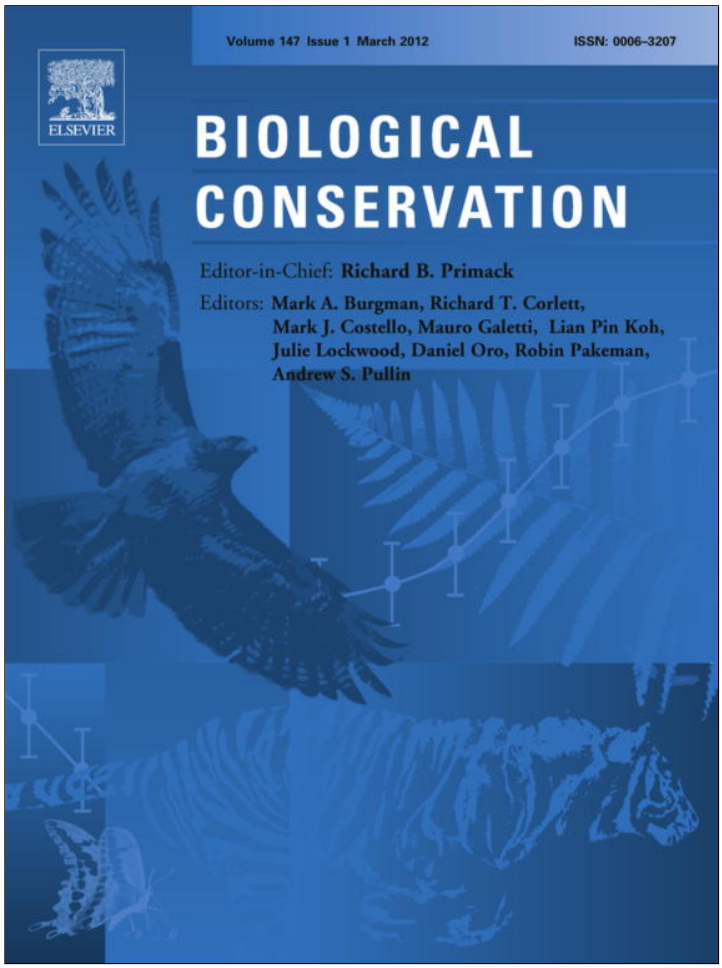

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Alpine flora may depend on declining frugivorous parrot for seed dispersal

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ABSTRACT

Globally, bird numbers are declining, with potentially serious flow-on effects on ecosystem processes, such as seed dispersal mutualisms. However, management to maintain seed dispersal may be inappropriate if unexpected animals are the most important dispersers. Numbers of the world's only alpine parrot, the New Zealand kea (*Nestor notabilis*), have declined drastically over the last 120 years after an intense period of official persecution. Today <5000 kea remain in the wild. Previously it has been assumed that like other parrots, kea would destroy most of the seeds they eat, thereby contributing little to seed dispersal. The New Zealand alpine flora is rich in fleshy-fruited species yet has a limited disperser fauna. Consequently, we investigated the relevance of kea as a seed disperser in New Zealand's alpine ecosystems. Field-based foraging observations coupled with faecal analyses showed kea were by far the most important extant alpine avian frugivore. Kea selected more fruiting species (21 vs. 17 species), consumed more fruit, and dispersed more seeds (8137 vs. 795) than all other birds combined. Rates of seed predation by kea were extremely low, and evident in only 25% of species eaten. Kea are the only species that make frequent long-distance flights within and between mountain ranges. Hence much of the effective long-distance dispersal of the alpine flora may be currently performed by kea. Conservation of kea is therefore important both for ensuring the survival of the species and for their role in seed-dispersal mutualisms for which there are few extant substitutes.

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SHORT NOTE

Frugivory and primary seed dispersal by a New Zealand falcon (*Falco novaeseelandiae*) at Red Tarns, Mt Sebastapol, New Zealand

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Raptors are primarily carnivorous but occasionally defecate seeds and therefore have the potential to act as seed dispersers. It is generally assumed that this is secondary dispersal rather than direct consumption of fruit by the raptor (Padilla & Nogales 2009). By depredating frugivorous animals such as birds and lizards, raptors can be important for seed dispersal and regeneration of plants through secondary dispersal mechanisms. Secondary seed dispersal is a multistep system that includes 2 or more dispersal processes, and can increase the distance that seeds are moved from the parent plant (Padilla & Nogales 2009). For example, on the Canary Is, seeds of *Rubia fruticosa* (Rubiaceae) are eaten by frugivorous lizards (primary dispersers) that are subsequently preyed upon by Eurasian kestrels (*Falco tinnunculus*), leading to secondary dispersal of seeds originally consumed by the lizards (Nogales *et al*. 2007). The Eurasian kestrel in this system is considered an important and effective long distance secondary seed disperser in 2 ways: 1) when it captures lizards and returns to the perch, the digestive tracts of the lizards are rejected with seeds intact; and 2) when lizard gut contents are occassionally ingested by the kestrel, some seeds are passed through intact (Nogales *et al*. 2007; Padilla & Nogales 2009).

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Globally, only 13 species of birds of prey, in 3 families, have been recorded consuming fruits (Galetti & Guimarães Jr. 2004), including some records of kites (eg. *Elanoides forficatus*) that directly consumed small berries and seeds with fleshy arils. In Guatemala, female barred forest-falcons (*Micrastur ruficollis*) have been observed feeding on the small fruits of *Tikalia prisca* (Sapindaceae) that fall to the forest floor (Thorstrom 1996). In Brazil, the crested caracara (*Caracaras plancus*) is known to consume and disperse the large, lipid-rich fruit of the palm *Attalea phalerata* (Palmae), and such behaviour has led to the suggestion that raptors may consume lipid-rich fruit to balance a protein-rich diet based on animal prey (Galetti & Guimarães Jr. 2004), a phenomenon which is also found in carnivorous arthropods (Pizo & Oliveira 2001).

The New Zealand falcon (*Falco novaeseelandiae*) is known to prey on mostly small birds, rodents and insects, and sometimes on small mammals and lizards (Fox 1977; Marchant & Higgins 1993; Seaton *et al*. 2008). The only published records of New Zealand falcons taking fruit are from captive individuals which were observed eating peaches, apples and tomatoes (Fox 1977). New Zealand falcon pellets have occasionally been found with seeds inside, but it has been assumed that these are ingested secondarily from the crops of granivorous (Fox 1977) and frugivorous prey birds (S. Kross, *pers. comm.*).

On 26 Mar 2010 at 0820 h, while carrying out behavioural observations on kea (*Nestor notabilis*) above the lower red tarns at Mt Sebastapol, Mt Cook National Park (43° 44.848'S, 170° 05.925'E), we saw an adult female falcon land on the ground ~30 m below our site and feed on the orange fruits of *Leucopogon fraseri* (Ericaceae) for 25 seconds. The falcon remained there for another 10 seconds and during this time defecated, and then it flew away. We then collected the faecal sac and counted 1 *Leucopogon fraseri* seed and 62 *Gaultheria depressa* (Ericaceae) seeds. All seeds were intact. Also present and identifiable were fruit skins and invertebrate remains.

Our observation describes the first evidence of frugivory by the New Zealand falcon. It is unclear whether this behaviour is restricted to alpine fleshy fruits, or even whether it is relatively common and widespread. However, our observations suggest that the potential for long distance dispersal of alpine seeds by falcons via both primary and secondary seed dispersal is possible. Given the paucity of extant dispersal agents in the alpine zone, New Zealand falcons could potentially be important seed dispersers for fleshy-fruited plants inhabiting open high-country ecosystems.

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LITERATURE CITED

Fox, N.C. 1977. The biology of the New Zealand falcon (*Falco novaeseelandiae* Gmelin 1788). Unpublished PhD thesis, University of Canterbury, Christchurch, New Zealand.

Galetti, M.; Guimarães Jr., P.R. 2004. Seed dispersal of *Attalea phalerata* (Palmae) by crested caracaras (*Caracaras plancus*) in the Pantanal and a review of frugivory by raptors. *Ararajuba 12:* 133-135.

Marchant, S.; Higgins, P.J. (eds) 1993. *Handbook of Australian, New Zealand and Antarctic Birds. Volume 2: Raptors to Lapwings.* Oxford University Press, Melbourne.

Nogales, M.; Padilla, D.P.; Nieves, C.; Illera, J.C.; Traveset, A. 2007. Secondary seed dispersal systems, frugivorous lizards and predatory birds in insular volcanic badlands. *Journal of Ecology 95*: 1394-1403.

Padilla, D.P.; Nogales, M. 2009. Behaviour of kestrels feeding on frugivorous lizards: implications for secondary seed dispersal. *Behavioural Ecology 20*: 872-875.

Pizo, M.A.; P.S. Oliveira. 2001. Size and lipid content of non-myrmecochorous diaspores: effects on the interaction with litter-foraging ants in the Atlantic rain forest of Brazil. *Plant Ecology 157*: 37-52.

Seaton, R.; Hyde, N.; Holland, J.D.; Minot, E.O.; Springett, B.P. 2008. Breeding season diet and prey selection of the New Zealand Falcon (*Falco novaeseelandiae*) in a plantation forest. *Journal of Raptor Research 42*: 256-264.

Thorstrom, R. 1996. Fruit-eating behavior of a barred forest-falcon. *Journal of Raptor Research 30*: 44.

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